Global change effects on the temporal dynamics of biodiversity, from species to communities : the example of plants and pollinators in Europe

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Par François Duchenne

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Dirigée par Élisa Thébault et Colin Fontaine

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Devant un jury composé de :

Ignasi Bartomeus	Researcher, EBD-CSIC	Rapporteur
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Ophélie Ronce	Directrice de recherche, ISEM	Examinatrice
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Élisa Thébault	Chargée de recherche, CNRS	Directrice de thèse
Emmanuelle Porcher	Professeure, MNHN	Invitée

Merci à mon père,
Compagnon de ces nombreuses aventures naturalistes,
Qui ont nourri ma passion pour le monde vivant.

« Tout enfant est un chercheur.
L'âge adulte fait souvent perdre cet étonnement, ces questionnements,
et on vit dans un monde rassurant car il est plus fait de réponses que de questions.
Faire de la recherche c'est conserver cette part d'enfance.
Les connaissances, les réponses sont rassurantes mais n'épuisent pas le questionnement. »
Jean-Claude Ameisen

« Pour les uns, qui voyagent, les étoiles sont des guides.
Pour d'autres elles ne sont rien que de petites lumières.
Pour d'autres qui sont savants elles sont des problèmes. »
Antoine de Saint-Exupéry, *Le Petit Prince*

« N'apprenons rien et le prochain monde sera identique,
avec les mêmes poids morts à soulever, les mêmes interdits à combattre... »
Richard Bach, *Jonathan Livigston le goéland*

A complex community. *Le Carnaval d'Arlequin* © Johan Miro.

Aknowledgements / Remerciements

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Réunion annuelle des voyeuristes ©Diane Gonzalez

Merci Benito pour ces moments passés à se plaindre que « l'été c'est fatiguant », pour ces quelques moments partagés sur le terrain avec tes fidèles cannetons, pour ta bonne humeur et ta joie de vivre. Merci au trio de Vieilles – Julie, Fanny et Anne – qui m'ont fait perdre une bonne partie de mes 3 ans de recherches en potins et autres discussions de femme en pleine crise de la ~~quarantaine~~ trentaine. Merci pour les attentions culinaires, et votre présence en cette fin de thèse. Deux générations nous séparent mais on s'est quand même bien marré ! Merfi à mamie, tantôt arpette tantôt maître, pour les parfums de rois, les histoires, les goûters et la recherche passionnée d'espèces

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Merci à cette belle équipe, car une thèse sans équipe, on sait tous comment ça se finit :

1ère année	2ème année	3ème année
		

« *Et, vous le savez bien maintenant, il n'y a rien de pire que l'espoir. Surtout dans le sport français.* »
#FFL (si tu travailles au lieu de regarder le Tour cultives toi en cliquant ici, si t'as la version papier t'es niqué)

Vous m'avez trainé dans les hauteurs, vous avez su me replacer dans le peloton pour éviter les bordures. On a tous peur de la défaillance en 3ème semaine, mais le CESCO c'est pas la FDJ, c'est bourré de vieux briscards qui en ont sous la pédale, merci à eux/elles.

Table of contents

I. Introduction

Ecology in face of the global change

Our world is experiencing an unprecedented global change in the history of humanity, strongly affecting biotic and abiotic components of the Earth system. A major part of these changes being driven by human societies, human imprint on the global environment has become so large that a new epoch in the Earth history has been proposed, the *Anthropocene* (Steffen *et al.* 2011). These changes have greatly accelerated on the second half of the 20th century (Steffen *et al.* 2006, 2011). Between 1960 and 2010, human population has been multiplied by more than two (United Nations 2019), urban areas have been increased by 1.6 (United Nations 2018), nitrogen fertilizer consumption have doubled in Europe and the USA (Grinsven *et al.* 2015), surface temperature has increased by 0.6°C (Masson-Delmotte *et al.* 2018), etc.. These anthropogenic changes are and will be affecting environmental conditions all around the world, as many of these changes are induced by global processes with a strong inertia and hysteresis[1]. In parallel, many studies report extinction rates 10 to 1000 times higher currently than pre-human levels, leading some authors to say that we are entering in the 6th mass extinction of the Earth history (Pimm *et al.* 1995; Wake & Vredenburg 2008; Barnosky *et al.* 2011; Ceballos *et al.* 2015). These extinctions are strongly linked to some previously mentioned global change drivers, such as land use change, climate change, nitrogen deposition, overexploitation or pollution (Sala *et al.* 2000; Brook *et al.* 2008).

A major challenge of our century is to assess how natural systems are and will be facing this accelerating global change. Ecology, defined as the *scientific study of the processes influencing the distribution and abundance of organisms, the interactions among organisms, and the interactions between organisms and the transformation and flux of energy and matter* (Likens 1992), is thus at the frontline of the challenges that global change imposes to human societies.

[1] "*After stabilization of the atmospheric concentration of CO2 and other greenhouse gases, surface air temperature is projected to continue to rise by a few tenths of a degree per century for a century or more, while sea level is projected to continue to rise for many centuries. The slow transport of heat into the oceans and slow response of ice sheets means that long periods are required to reach a new climate system equilibrium.*

Some changes in the climate system, plausible beyond the 21st century, would be effectively irreversible. For example, major melting of the ice sheets and fundamental changes in the ocean circulation pattern could not be reversed over a period of many human generations."

IPCC, *Climate Change 2001: Synthesis Report*

Ecology has investigated global change effects on biodiversity mainly through three angles of research: population or species-centered, describing species responses to global change drivers, evolutionary, evaluating the effect of global change on evolutionary trajectories of species, and functional, assessing effects of global change on ecological functions and services. These three research axes cover the diverse levels of organization of ecological systems, from species to ecosystems, but we still struggle to build bridges among them and to understand how changes at a given level of organization combine to affect the higher level of organization and vice versa. In the following part of the Introduction, I will briefly review the current knowledge regarding global change effects at the species and community level, before presenting some current knowledge gaps in these fields, and finally I will present issues that I tried to tackle during this PhD. In the following parts of this manuscript, the first person singular ("I") will be used for sections that mainly involve personal reflections and choices while the first person plural ("we") will be used for sections that involve collaborative projects.

Species responses to global change

As global change is affecting environmental conditions with a high velocity, it likely creates mismatch between phenotypes and environment for many traits of many species, which can impact species persistence (Radchuk *et al.* 2019), defined here as the average time until species extinction. To maintain an adequate match between their phenotypes and the environment, species have three main ways to respond under such change (**Figure I-1**): they can track their optimum in space (geographic range shift) and/or in time (phenological shift) if it is possible, and/or they can respond adaptively in another way to survive and reproduce in a modified environment, i.e. modify their optimum, (Bellard *et al.* 2012). In this part I will briefly review what is known about geographic range and phenological shifts, before reviewing evidence of their links with species persistence in a changing world.

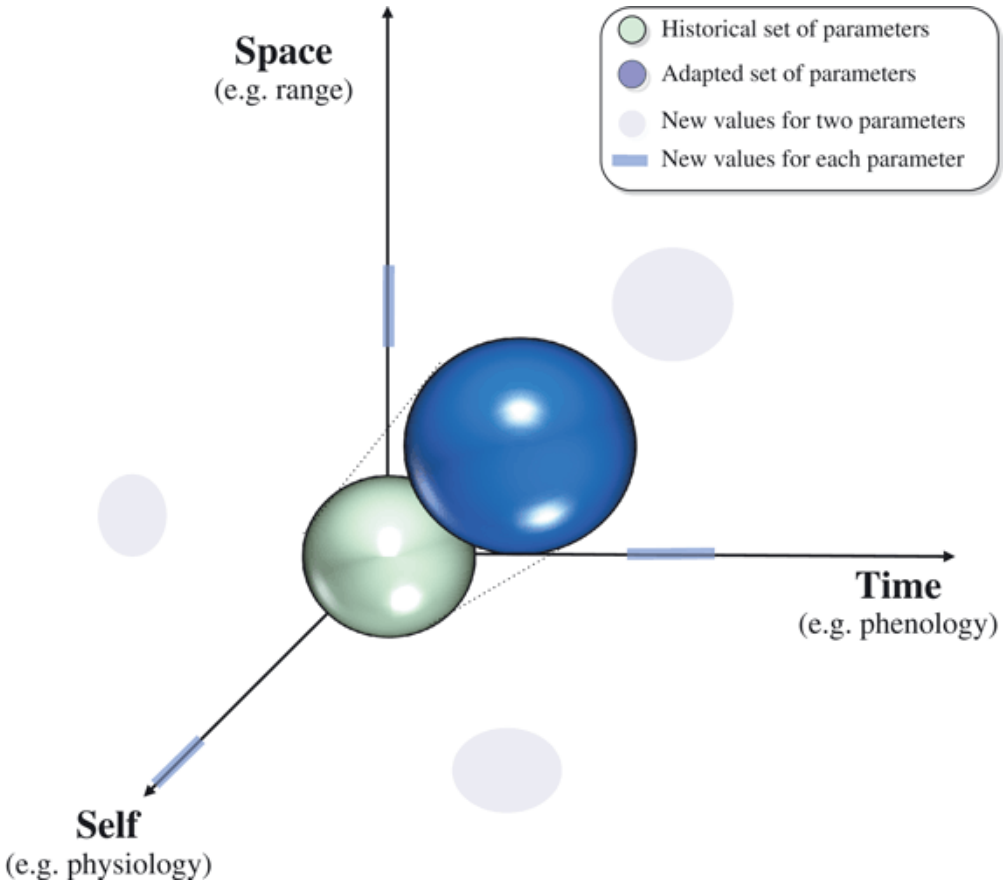

Figure I-1: ***The three directions of responses to climate change through phenotypic plasticity or evolutionary responses****. Moving in space (dispersing to areas with suitable habitat or changing location on a microhabitat scale), shifting life history traits in time (adjusting life cycle events to match the new climatic conditions, including phenology and diurnal rhythms), or changing life history traits in its physiology to cope with new climatic conditions. Species can cope with climate change by shifting along one or several of these three axes. Extracted from Bellard et al. (2012).*

Shifts in geographicl range and phenology

Average shifts in space and time

Geographic range shifts correspond to a change in distribution along one of the three following dimensions: latitude, longitude and elevation/depth (Lenoir & Svenning 2015). As temperature increases over time, we expect poleward and upward geographic range shifts for terrestrial species, which would allow species to maintain constant experienced climatic conditions over time by tracking spatially their climatic optimum (Parmesan 2006). Thus, in a context of climate warming, these geographic range shifts are expected to be towards higher latitudes or elevation in terrestrial ecosystems. Such changes have been shown at the end of the

20th century, from changes in species composition in local communities (Smith 1994; Barry *et al.* 1995) to geographic range shifts in occurrence data for individual species (Parmesan 1996, 2006; Parmesan *et al.* 1999; Thomas & Lennon 1999). Now, geographic range shifts have been reported in terrestrial and aquatic ecosystems and in many taxonomical groups, such as insects (Parmesan *et al.* 1999; Devictor *et al.* 2012), birds (Devictor *et al.* 2012), vascular plants (Lenoir *et al.* 2008), algae (Wernberg *et al.* 2011), amphibians (Pounds *et al.* 1999; Lenoir *et al.* 2020), mammals (Williams & Blois 2018), reptiles (Pounds *et al.* 1999; Moreno-Rueda *et al.* 2012). Although species are moving, most studies show that species (Monsinjon *et al.* 2019; Lenoir *et al.* 2020) and communities (Menéndez *et al.* 2006; Bertrand *et al.* 2011, 2016; Devictor *et al.* 2012) are lagging behind climatic isocline shifts, and only few studies show that species shift their range fast enough to follow their climatic optimum (Chen *et al.* 2011) or even sometimes overshoot expected shifts (Bässler *et al.* 2013). The most recent review shows that, on average, terrestrial species are moving towards higher latitudes with a velocity of 1.11 ± 0.96 km.yr^{-1} and upslope with a velocity of 1.78 ± 0.41 m.yr^{-1}, which is far below isotherm shifts (Lenoir *et al.* 2020).

In addition to moving in space, species are also tracking their climatic optimum in the season through phenological shifts. Here, we defined phenology as *a repeated seasonal life-cycle event such as annual migration or spawning* (Letcher 2009). Consequently, phenological shift is a general term corresponding to any change in the seasonal timing of any seasonal life-cycle event. The first studies showing that phenological shifts are occurring because of climate change was published in the same period than the first piece of evidence of geographic range shifts. Aldo Leopold's[2] observations from Wisconsin gave us one of the first evidence that a wide diversity of spring phenological events, such as bird migration return and plant flowering blooms, are occurring earlier by 0.12 day per year in average, reflecting climate change (Bradley *et al.* 1999). Then numerous studies have shown that many phenological events are taking place earlier because of climate change: plant flowering period (Fitter & Fitter 2002), bird breeding time (Dunn & Winkler 1999), insect flight period (Roy & Sparks 2000), calling period of frogs (Gibbs & Breisch 2001), phytoplankton spring bloom (Winder & Schindler 2004), etc. These phenological shifts have been widely reviewed (Parmesan 2006, 2007) and

[2] « *Un siècle a passé depuis que Darwin nous livra les premières lueurs sur l'origine des espèces. Nous savons à présent ce qu'ignorait avant nous toute la caravane des générations : que l'homme n'est qu'un compagnon voyageur des autres espèces dans l'odyssée de l'évolution.* » Aldo Leopold, *Almanach d'un comté des sables*

mainly concern spring events, which take place earlier in average by 2.8 days per decade in the northern hemisphere (Parmesan 2007). Autumnal events are largely overlooked and exhibit more contrasted results (Gallinat *et al.* 2015): the few autumnal studies reveal that leaf senescence of plants, migration of short-distance birds and diapause of insects seem delayed because of temperature increase while fruit ripening and departure of long-distance migrant birds have advanced (Gallinat *et al.* 2015).

Interactive effects of multiple drivers

These shifts are often assumed to be driven by temperature change, but some studies have shown more complex patterns, revealing that other drivers can interact with temperature to drive geographic range and phenological shifts. First, climate change does not imply only temperature increase but also shifts in precipitation regime for example, which affects habitats in many other ways. For example, it happens sometimes that temperature and precipitations imply opposite selection pressures. In mountainous regions, where temperature and precipitation exhibit opposite gradients, downhill spatial shifts driven by precipitations have been observed (Crimmins *et al.* 2011) and some phenological shifts, such as shifts in plant fruiting and leaf unfolding, are driven by rainfall changes rather than by temperature increase (Peñuelas *et al.* 2004). Second, as the spatial and seasonal distribution of living organisms is strongly constrained by inter-specific interactions (Wisz *et al.* 2013; Rudolf 2019), such as competition or facilitation, interactions between species can affect the velocity of geographic range shifts (Svenning *et al.* 2014) and even drive geographic range or phenological shifts opposite to temperature pressure (Lenoir *et al.* 2010; Rudolf 2019). Finally, landscapes, which are strongly affected by land use change, also determine geographic range and phenological shifts. Regarding range shifts, moving in space requires that species have dispersal abilities. Landscape habitats have been shown to affect the ability of species to follow their climatic optimum over space (Pöyry *et al.* 2009; Gaüzère *et al.* 2017). Consistently with that, species from freshwater or marine habitat are better tracking climatic conditions than species from terrestrial and standing water systems (Hof *et al.* 2012; Lenoir *et al.* 2020), likely due to the dispersal easiness in such aquatic habitats. Regarding phenological shifts, urbanization interacts with baseline climatic conditions, contributing to advance plant phenological events in cold areas but delaying them in warm areas (Li *et al.* 2019). Such kind of interaction between urbanization and climate has also been observed for insect phenology (Diamond *et al.* 2014).

Geographic range and phenological shifts can be driven or mediated by other global change drivers than climate warming, but many studies find patterns that are consistent with processes driven by temperature (Parmesan 2006, 2007; Bartomeus *et al.* 2011; Hodgson *et al.* 2011; Lenoir & Svenning 2015; Cohen *et al.* 2018). However, most of these studies often focus only on climate change, neglecting putative confounding effects with other drivers. At first sight, the last global meta-analysis on geographic range shifts shows that the global patterns are consistent with what is expected from climate warming: shifts are generally toward higher elevation and latitude, with stronger shifts in the Northern Hemisphere than in the southern one (marginally significant), as expected from differences in velocity of climate change, and stronger geographic range shifts in ectotherms than in endotherms (Lenoir *et al.* 2020). But the same study also shows that the human footprint index and the kind of ecosystem (ocean *vs* land) strongly determine the ability of species to follow their historical climatic conditions, stressing the need to jointly study the effects of several global change drivers on shifts in geographic range and phenology.

Changes in shape or extent of geographic and seasonal ranges

Existing studies have mainly focused on directional shifts in the centroid of the geographic range or in the average event date while a wide diversity of shifts, such as changes in shape or extent of the geographic and seasonal ranges, remain overlooked. Indeed, in addition to the directional shifts in geographic range and phenology, the shape and the extent of the geographic and seasonal ranges, measured at the species/population level, can also change because of climate change (Høye *et al.* 2013; Lenoir & Svenning 2015; CaraDonna *et al.* 2017; Hällfors *et al.* 2020). For example, in Great-Britain, some birds have extended their range northwards but persist at southern margins of their geographic ranges, thus realizing an overall expansion of their range (Thomas & Lennon 1999). The fact that leading and trailing edges of the geographic/seasonal range can change in distinctive ways or with distinctive strengths (CaraDonna *et al.* 2014) leads to a wide diversity of geographic range and phenological shifts (**Figure I-2**). This diversity of responses has been recently highlighted, with about a fourth of plants and a third of birds exhibiting changes in phenology duration (CaraDonna *et al.* 2014; Hällfors *et al.* 2020). However, it still remains poorly studied because of methodological difficulties. The main difficulty for geographic range shifts, is that such studies would require to have dataset that encompass all the species distribution, and not only a small part or margins as it is often the case (Parmesan 2006). Regarding phenological shifts, characterizing changes

in the seasonal duration of events in addition to seasonal shifts require to have data that properly reflects phenological changes, because estimated date of onset and end of a phenological event strongly depends on sampling effort and/or abundance changes, in contrast to the average date (CaraDonna *et al.* 2014). Thus, jointly model shifts in duration and average date of phenological events would require to use new statistical methods allowing to take into account those putative bias.

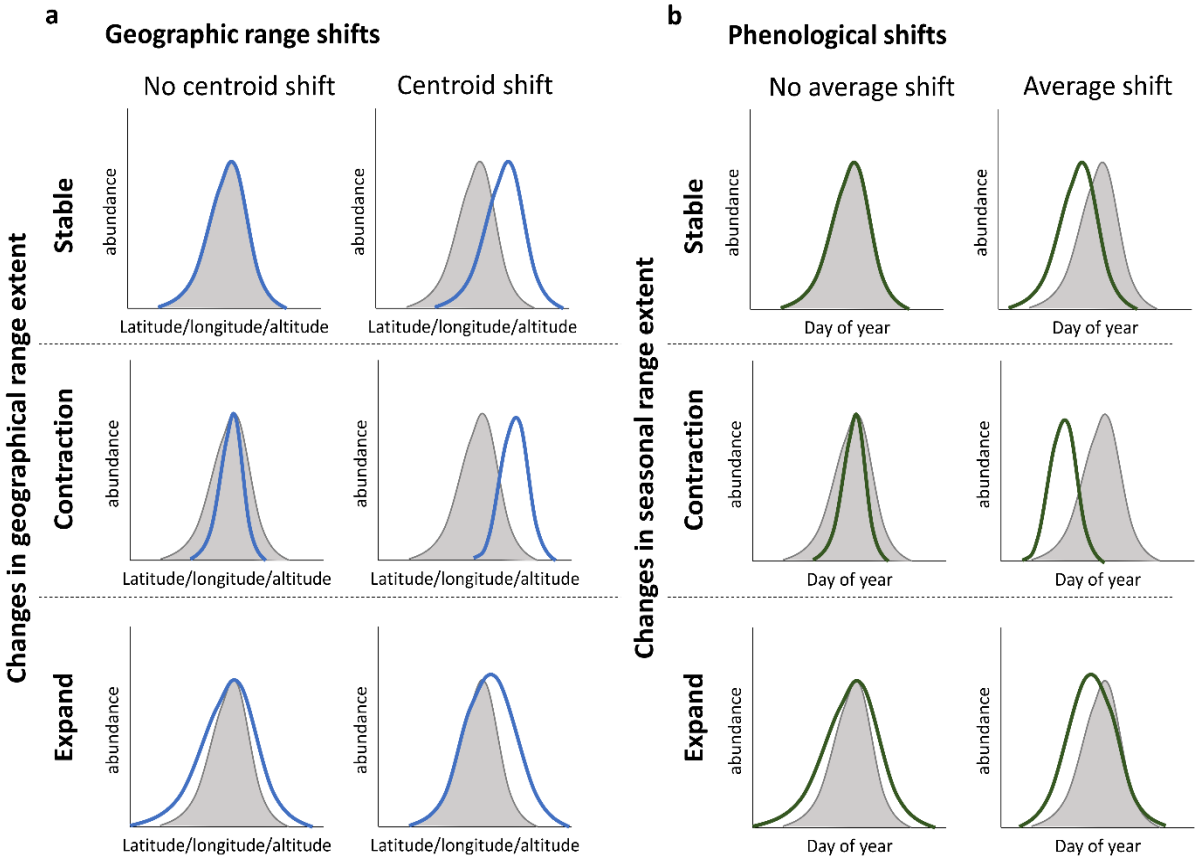

Figure I-2: ***Examples of diverse geographic range and phenological shifts.*** *(a) geographic range shifts and (b) phenological shifts, as a function of the centroid/average shifts and of the changes in the range extent. Grey areas represent the historical spatial/seasonal distributions at the population level, while colored lines represent the current distributions. For simplicity we used shifts in one dimension instead of the 3 dimensions used for geographic range shifts. Modified from Lenoir & Svenning (2015) and Hällfors et al. (2020).*

Species persistence in a changing world

Overall declines in species persistence

Many studies have shown a strong decrease in biomass, abundance or richness of many eukaryotic taxa because of global change: arthropods (Hallmann *et al.* 2017; Seibold *et al.* 2019), amphibians (Collins *et al.* 2009), birds (Donald *et al.* 2001; Stanton *et al.* 2018), mammals (Craigie *et al.* 2010; Spooner *et al.* 2018), corals (De'ath *et al.* 2012). Those decline are leading to very high rates of extinction relatively to pre-human levels (Pimm *et al.* 1995; Wake & Vredenburg 2008; Barnosky *et al.* 2011; Ceballos *et al.* 2015), 27% of the assessed species by the International Union for Conservation of Nature being threatened of extinction (IUCN 2020). All these elements suggest that the persistence (i.e. the time until extinction) of many eukaryotic species is currently decreasing because of very fast changes in many earth system variables (Steffen *et al.* 2006), including land-use, climate and chemical pollutants, which are considered as the main threats for biodiversity (Sala *et al.* 2000). Although there is a substantial heterogeneity among species in abundance changes in response to global change, hidden behind this average decline, the percentage of species benefiting to global change seems relatively low, between 5% and 30% of the species depending on the groups and locations studied (McKinney & Lockwood 1999). Recent results on plants (Martin *et al.* 2019), amphibians (Kafash *et al.* 2018), insects (Herrera *et al.* 2018), birds (Tayleur *et al.* 2016) show that those winners (species having positive average population trends) are often thermophile species, while losers (species having negative average population trends) are often cold-dwelling species, suggesting that climate change is an important driver of changes in species persistence.

Species persistence and the shifts in geographic range and phenology

Considering that climate change is likely one of the main driver of species persistence, keeping pace with historical climatic conditions (i.e. climatic conditions before fast anthropic climate change, assumed to be optimal ones) should preserve species from decline and thus maintain species persistence. Indeed, it is widely assumed that geographic range and phenological shifts allow to maintain an adequate match between species phenotypes and the environment, and thus are considered as adaptive responses (i.e. increase individual fitness or

species persistence) to climate change. However, since species struggle for existence[3] (Darwin 1859), consequences of geographic range and phenological shifts on species persistence are often difficult to anticipate, because they do not only depends on tracking climatic optimum but are mediated by inter-specific interactions, such as competition (Alexander *et al.* 2015; Rudolf 2019). Thus, while many studies assume that species shifting their geographic range slower than climatic isotherm shift pay a demographic cost (Bertrand *et al.* 2011; Dullinger *et al.* 2012), we still lack empirical evidence of such demographic cost. Indeed, simultaneous estimation of past geographic range shifts and species persistence are very scarce and often regard a small number of species (Parmesan *et al.* 1999; Thomas & Lennon 1999; Grenouillet & Comte 2014). To investigate this overlooked question, Lenoir & Svenning (2015) have proposed a two dimensional approach, comparing the observed shifts in geographic range with a measure of species persistence based on the extent of species geographic range itself (Lenoir & Svenning 2015), as presented in **Figure I-2a**. In that case, species persistence is measured as a change in the extent of species geographic range, a contracting range implying a decrease of species persistence and vice-versa (He & Gaston 2003). Although such framework has been proposed a few years ago, assessments of the relationships between geographic range shifts and species persistence at large spatial scale remain limited to few species, stressing the need to develop such approaches.

Regarding phenological shifts, a few studies on well-studied systems, such as bird breeding season and plant flowering period, assess the relationships between phenological shifts and individual fitness. These studies show that phenological shifts are adaptive (i.e. increase individual fitness or species persistence) but insufficient to track optimums (Radchuk *et al.* 2019). Moreover, studies on birds show that populations of migratory bird species that did not show a phenological response to climate change are declining (Moller *et al.* 2008), suggesting that absence of phenological shifts can partially drive species decline. By setting aside birds, few studies have been designed to assess if phenological shifts are adaptive or not. Phenological

[3] "*I use this term in a large and metaphorical sense including dependence of one being on another, and including (which is more important) not only the life of the individual, but success in leaving progeny. Two canine animals, in a time of dearth, may be truly said to struggle with each other which shall get food and live. But a plant on the edge of a desert is said to struggle for life against the drought.... As the mistletoe is disseminated by birds, its existence depends on birds; and it may metaphorically be said to struggle with other fruit-bearing plants, in order to tempt birds to devour and thus disseminate its seeds rather than those of other plants. In these several senses, which pass into each other, I use for convenience sake the general term of struggle for existence.*" Charles Darwin, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*

shifts are often assumed to be driven by phenotypic plasticity to temperature, as shown for birds, which track the advancing abundance peak of caterpillars thanks to an adaptive phenotypic plasticity to spring temperature (Nussey *et al.* 2005; Charmantier *et al.* 2008). As such phenotypic plasticity to temperature is a common feature of many life cycle events, such as activity periods of amphibians (Phillimore *et al.* 2010), butterflies (Roy *et al.* 2015), bees (Fründ *et al.* 2013) and flowering period of plants (Anderson *et al.* 2012), that could explain why phenological shifts are generally related to climate warming. However, some studies have shown that such phenotypic plasticity to temperature can be either neutral, not increasing species persistence (Frei *et al.* 2014), and even sometimes maladaptive, decreasing species persistence (Dyck *et al.* 2015). Thus, uncertainty remains if observed phenological shifts in response to climate warming are adaptive or not, because in many case we are not able to assess it. Indeed, we often have access to long-term trends in environmental variables as well as in phenotype values, allowing to determine phenotypic plasticity to environmental variables (**Figure I-3a-c**), but we often miss fitness measures allowing to determine if such phenotypic plasticity is adaptive or not (**Figure I-3d-f**). Such fitness-phenotype relationships are available only for few long-term monitored populations, such as the few used to study bird breeding phenology (Radchuk *et al.* 2019) or plant flowering phenology (Ehrlén & Valdés 2020). Furthermore, few studies on plant flowering phenology (Anderson *et al.* 2012; Ehrlén & Valdés 2020), bird breeding phenology (Ramakers *et al.* 2019) and insect hatching (Asch *et al.* 2013) show that phenotypic plasticity to temperature is not the only driver of phenological shifts. Indeed, these studies show that evolution is occurring because of selection pressures due to interspecific-interactions, and it is partially driving observed phenological shifts. Such results suggest that phenotypic plasticity to temperature alone is a not enough to track ecological optimums in time potentially because of inter-specific relationships (Alexander & Levine 2019; Loeuille 2019) or because phenotypic plasticity is more a developmental constraint than an adaptive response (Dyck *et al.* 2015). Thus, the adaptive nature of phenological shifts remains widely unknown, partly because we are largely ignorant about the mechanisms driving them.

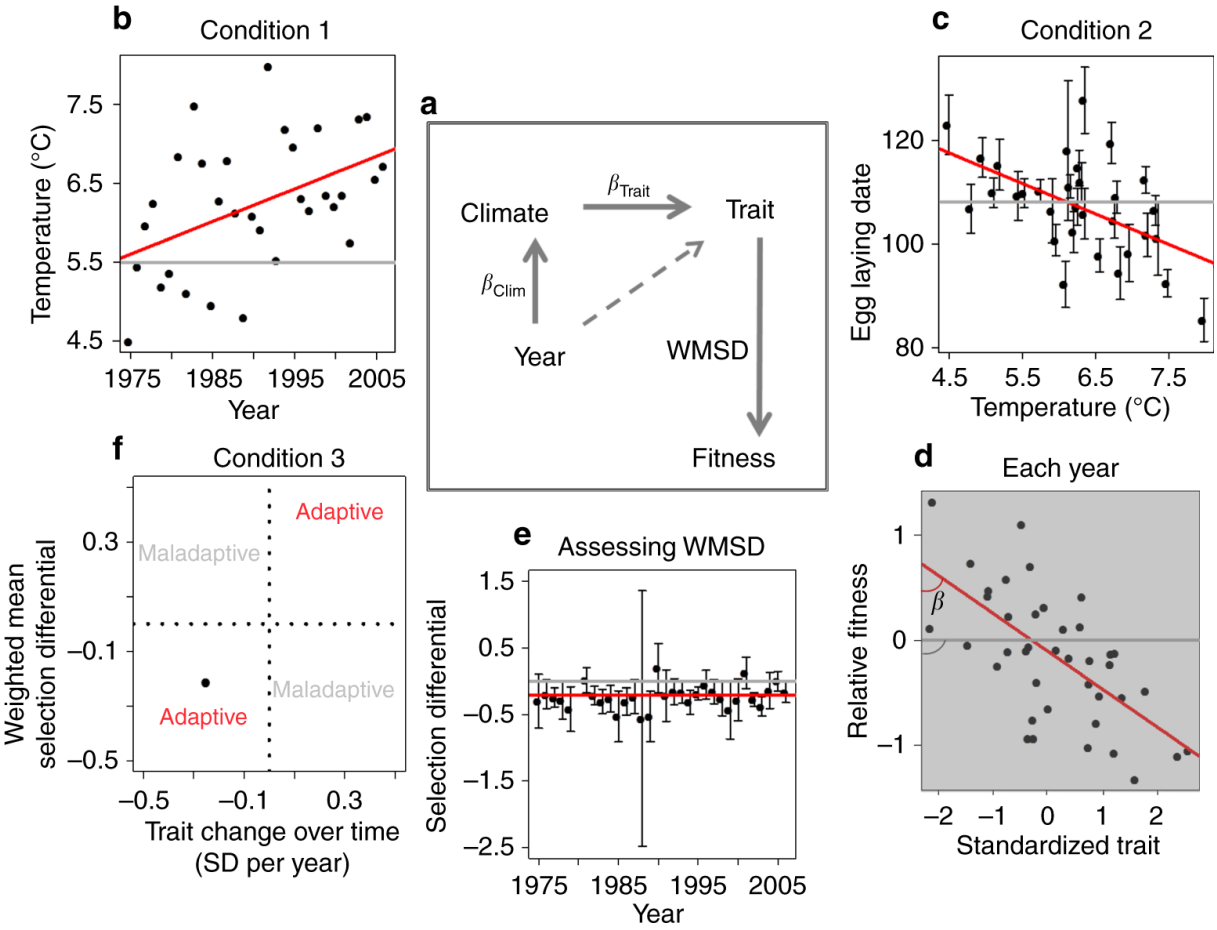

Figure I-3: ***A framework for inferring phenotypic adaptive responses using three conditions***. ***a*** *General framework. Arrows indicate hypothesized causal relationships, with dashed arrow indicating that we accounted for the effects associated with years when assessing the effect of climate on traits.* ***b–f*** *demonstrate steps of the framework using as an example one study from Radchuk et al. (2019) dataset.* ***b*** *Condition 1 is assessed by* β_{Clim}*, the slope of a climatic variable on years,* ***c*** *Condition 2 is assessed by* β_{Trait}*, the slope of the mean population trait values on climate.* ***d*** *Interim step: assessing the linear selection differentials (β). Note that each dot here represents an individual measurement in the respective year and not a population mean.* ***e*** *To assess condition 3, first the weighted (by the invert of the standard error associated with estimates) mean annual selection differential (WMSD) is estimated.* ***f*** *Condition 3 is then assessed by checking whether selection occurs in the same direction as the trait change over time, calculated as the product of the slopes from conditions 1 and 2. Red lines and font in* ***b–f*** *illustrate the predictions from model fits. Grey lines and font illustrate the lack of effect in each condition. As an example, if temperature increased over years (as shown by the red line in* ***b****), phenology advanced (depicted by the red line in* ***c****) and WMSD was negative (as depicted by the red line in* ***e****), then fitness benefits are associated with phenological advancement, reflecting an adaptive response (point falls in quadrant 3 in* ***f****). Extracted from Radchuk et al. (2019).*

Species responses to global change in a community framework

A classical definition of ecological communities could be a definition from Robert Whittaker (Whittaker 1975), *an assemblage of populations of different organisms that live in an environment and interact with one another, forming together a distinctive system with its own composition, structure, environmental relations, dynamic and functions*, but here we simply define ecological communities as a collection of interacting species found in a particular location at a given time period (Morin 1999). Community ecology is the study of patterns and processes involving at least two species co-occurring in space and time and interacting (Morin 1999), a very broad definition that embraces a large part of Ecology[4]. Since communities are constituted from a set of species and a set of interactions among species, which depends on species co-occurrence in space and time, any changes in spatial or temporal distributions of species is supposed to affect ecological communities by affecting not only the species composition of ecological communities but also interactions among them. Reciprocally, because species are linked by interactions, communities affect eco-evolutionary trajectories of species, and thus the way that they respond to global change. Here I will first briefly review the current knowledge on the properties of ecological communities, mainly focusing on their stability and ecological dynamics. Then I will present what we know about how species responses to global change combine to affect communities. Finally, I will review our knowledge about how species responses to global change are affected by inter-specific interactions.

Community stability and structure

Community stability and the structure of ecological interaction networks

Based on Darwin' statement on the struggle for existence among species, the competitive exclusion principle predicting species exclusion when ecological niche are too close (Volterra 1928; Gause 1934) laid the foundation stone of a key challenge of Ecology: understand what stabilizes ecological communities and prevent them from collapse. In this topic, few papers have stimulated as much debate and research in Ecology as Robert May's paper in *Nature* in

[4] "*Ecology is the science of communities. A study of the relations of a single species to the environment conceived without reference to communities, and in the end, unrelated to the natural phenomena of its habitat and community associations is not properly included in the field of ecology.*" Victor Shelford, *Laboratory and Field Ecology. The Responses of Animals as Indicators of correct Working Methods*

1972, *Will a Large Complex System be Stable?*, at the origin of one of the most beautiful research story of Ecology, the ongoing Diversity-Stability debate. Based on a work from Gardner & Ashby, which shows by using numerical simulations that the probability of a system to be stable decreases with its connectance (i.e. number of realized links divided by the number of possible links) and its number of entities (Gardner & Ashby 1970), May completed this work by an analytical approach, showing that connectance and diversity predict pretty well the probability of stability of communities (May 1972).

Table I-1: *definitions of stability. Modified from McCann (2000).*

	Term	Definition
Definition of dynamic stability	Equilibrium stability	Can be a discrete measure that considers a system stable if it returns to its equilibrium after a small perturbation away from the equilibrium. For randomly constructed communities, can be a continuous measure representing the prevalence of stable points, alternative stable states, and nonstationary attractors.
	General stability	A measure which assumes that stability increases as the lower limit of population density moves further away from zero. Under non-equilibrium dynamics, such limits to population dynamics generally imply a decrease in population variance (see variability definition below). In theory, for systems with nonpoint attractors, stability can be view as the prevalence of cyclic versus chaotic attractors.
	Variability	The variance in population densities over time, usually measured as the coefficient in variation. Common in experimental tests of stability.
Definition of resilience and resistance stability	Equilibrium resilience	A measure of stability that assumes system stability increases as time required to return to equilibrium decreases after a perturbation. A rapid response means that a system recoils rapidly back to its equilibrium state.
	General resilience	A measure of stability that assumes system stability increases as return time to the equilibrium/non-equilibrium solution decreases after a perturbation. A rapid response means that a system recoils rapidly back to its equilibrium/non-equilibrium state.
	Resistance (or Robustness)	A measure of the degree to which a variable changes after a perturbation. Can be a continuous measure, such as changes in mean combined densities or a number of extinctions after a press or pulse perturbation. Can be a discrete measure that assesses a community's ability to resist invasion (that is, if an invader fails, the community resists invasion).

These theoretical conclusions then seem to contradict the previous ones, which suggest that the more diverse the ecological systems, the less they are affected by invasions and extinctions

(MacArthur 1955). In an attempt to resolve the issue, many empirical studies have been conducted and find contrasting results (McCann 2000; Ives & Carpenter 2007), but 69 % of the 64 studies reviewed by Ives & Carpenter (2007) have found a positive relationships between diversity and stability. However, such apparent contradiction between theoretical and empirical results is partly due to the diversity of stability concepts (**Table I-1**) rather than real oppositions among these results. While MacArthur, and more generally empirical studies, uses stability to refer to the variability in species abundances, May uses stability to refer to the probability to reach a stationary attractor (McCann 2000). Considering this mismatch between empirical and theoretical studies, it is almost impossible to merge both and to draw conclusions, that *reemphasizes the need to statistically fit models to data*[5] (Ives & Carpenter 2007). The theoretical approach of stability of May also neglects an important aspect of the diversity-stability relationship: the feasibility, which is the fact that all species have strictly positive abundances at equilibrium. Considering only feasible equilibria in the analysis reverses the relationship found by May, leading to a positive relationship between diversity and stability (Roberts 1974). However, feasibility in diverse system also exhibit a strong negative relationships with diversity (Dougoud *et al.* 2018). Considering feasibility thus reinforce the diversity-stability debate rather than solve it (Dougoud *et al.* 2018) and focusing on the theoretical definitions of the stability, mainly equilibrium stability and resilience (**Table I-1**), the original question asked by May's article remains unchanged: why are diverse ecological communities stable while theory predicts that they should not be?

A few elements of answer are given at the end of May's article, which says: "*within a web species which interact with many others [...] should do so weakly [...], and conversely those which interact strongly should do so with but a few species"* and "*our model multi-species communities, for given average interaction strength and web connectance, will do better if the interactions tend to be arranged in 'block'"* (May 1972). Indeed, Ecology has found some mechanisms promoting stability of complex ecological communities by remembering that *Nothing in Biology Makes Sense Except in the Light of Evolution* (Dobzhansky 1973) and that

[5] "*This suggests that the preponderance of empirical studies showing positive relationships (43 of 64, table S2) do so because they use definitions of stability that are likely to show positive relationships. Nonetheless, theory generally predicts negative diversity stability relationships for stability measured as return rates, yet eight of the nine empirical studies that used this measure reported a positive or no relationship (table S2). Given the frequent mismatches between empirical studies and theory, we think it is difficult to draw any strong conclusions from the empirical studies. This reemphasizes the need to statistically fit models to data.*" Ives & Carpenter (2007)

natural systems are evolved systems, not random associations of species. To do so, ecological communities are often represented by using networks, a mathematical representation of interacting species in which species are the nodes and interactions the links. First, stabilizing patterns have been found in the non-random distribution of interactions strengths among species (Yodzis 1981). Food webs are largely stabilized by an over-representation of weak interactions (McCann *et al.* 1998), especially in long loops (Neutel *et al.* 2002, 2007), and by the fact that interaction strengths are distributed following constraints determined by species body sizes (Otto *et al.* 2007; Jacquet *et al.* 2016). Second, echoing May's prediction, empirical food webs tend to exhibit a high modularity, food webs exhibit a highly modular compartmentation of interactions, which are organized in blocks of interactions (Melián & Bascompte 2004; Fontaine *et al.* 2011). Despite opposite results found by abstract and theoretical models (Allesina & Tang 2012; Allesina *et al.* 2015) a majority of studies found that the structure of empirical networks, defined by the distribution of interaction strength and the organization of occurring interactions, provide higher stability than random ones (Kondoh 2008; Thébault & Fontaine 2010; Tang *et al.* 2014), allowing diverse but stable systems existing. However, those researches first focused only on trophic interactions, while many other kinds of interaction shape communities, such as mutualistic ones, in which both partners benefit from the interaction.

The study of mutualistic interactions in communities has been achieved using bipartite graphs to represent two distinct guilds of organisms interacting together (**Figure I-4**), instead of a representation of communities as undirected graphs as for food webs, allowing to represent several trophic levels (Bascompte & Jordano 2006). Bipartite graphs, or bipartite networks, can be represented as an interaction matrix, which differs from the classical adjacency matrix used for food webs, in which each column represents a species from the first guild, while each row represents a species from the second guild (**Figure I-4**). Using such representation, it has been shown that mutualistic networks are nested, a structure that occurs when specialist species tend to interact with a proper set of the species that interact with more generalist ones (Bascompte *et al.* 2003). In mutualistic networks, the analysis of network structure has mainly been conducted on pollination networks, although other kinds of networks have been considered, such as seed dispersal networks. This might be because the interaction among pollinators, mainly insects, birds and bats, and flowering plants imply very diverse groups in terms of species and because 87% of terrestrial plants, a basal trophic level of a majority of terrestrial ecosystems, depends on this interaction to reproduce (Ollerton *et al.* 2011). In contrast bipartite

antagonistic networks, which describe predation interactions, are less nested than expected and highly modular (Fontaine *et al.* 2011). Nestedness and modularity have been shown to promote stability (Thébault & Fontaine 2010) and diversity (Bastolla *et al.* 2009; Thébault & Fontaine 2010) of mutualistic and antagonistic networks respectively, showing that mechanisms stabilizing networks depends on the kind of interactions constituting them.

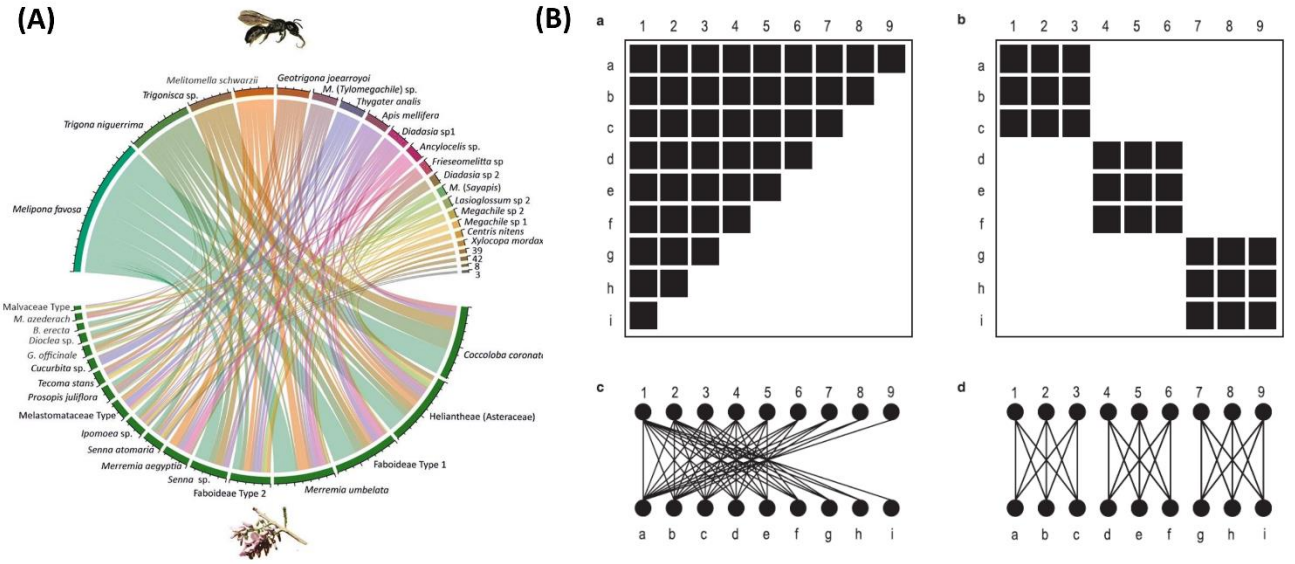

Figure I-4: ***Bipartite networks.*** ***(A)*** *An example of quantified mutualistic interaction network: a bee-plant interaction network in a forest of the Colombian Caribbean (Flórez-Gómez et al. 2020). Extracted from Flórez-Gómez et al. (2020).* ***(B)*** *Schematic representation of perfectly nested (a) and (c) and modular (b) and (d) binary bipartite networks. (a) and (b) Matrix representation, where each row and column represents a species, and the intersections of rows and columns are black when the species interact. (c) and (d) Network representation, where each circle (or node) represents a species, which are connected by edges when the species interact. Extracted from Fontaine et al. (2011).*

Traits and phenology as determinants of network structure

Since the community structure plays an important role in stability-diversity relationships, the linkage rules (i.e. rules defining species interactions) at the base of the structural properties of networks have been investigated during the last decade. Although some studies have found that the abundance of species is an important determining factor of species interactions (Vázquez *et al.* 2007), food webs and mutualistic networks also exhibit interaction distributions that depend on the evolutionary history of species (Rezende *et al.* 2007; Eklöf *et al.* 2012; Laigle *et al.* 2018), suggesting that long-term coevolution processes among species traits is at the base of patterns observed. In pollination networks, the first studies have mainly focused on the importance of morphological traits in shaping the structure of pollination networks, maybe

because of an historical heritage, since Charles Darwin predicted the existence of a unknown pollinator from floral morphology (Darwin 1862). These works on morphological traits have shown they participate to structure pollination networks more than species abundance and promote nestedness (Santamaría & Rodríguez-Gironés 2007; Chamberlain *et al.* 2014; Watts *et al.* 2016; Biddick & Burns 2018). These studies also highlight that forbidden links, defined as impossible interactions among species due to incompatible traits, play an important role in pollination network structure (Santamaría & Rodríguez-Gironés 2007; Vizentin-Bugoni *et al.* 2014).

However, those studies used empirical data, aggregating observed interactions in time and space, while recent studies have shown that interaction networks are dynamic over space and time. Indeed, the few studies with seasonal sampling in pollination networks show that the seasonal turnover of interactions is high (CaraDonna *et al.* 2017; Souza *et al.* 2018; Rabeling *et al.* 2019), leading to seasonal changes in network structure (Rabeling *et al.* 2019; CaraDonna & Waser 2020), and suggesting that phenology is an important factor in community structure. Indeed, several studies including phenology in addition to morphological traits have shown that phenology is often the best predictor of plant-pollinator interactions (Junker *et al.* 2013; Maruyama *et al.* 2014; Gonzalez & Loiselle 2016; CaraDonna *et al.* 2017). Despite the importance of phenology for pollination interactions, the way that species are organized along the season, henceforth the seasonal structure of ecological communities, remains widely overlooked, theoretically as well as empirically. There are only few preliminary works on pollination networks linking seasonal structure to community diversity, network structure and robustness to extinctions (Encinas-Viso *et al.* 2012; Ramos–Jiliberto *et al.* 2018).

Thus, we currently know that ecological communities can be diverse and stable because of structural patterns that are non-random and stabilizing. However, linkage rules underlying these patterns remain unclear and taking into account the seasonal dynamic of communities seems an important step to highlight mechanisms structuring interactions networks, and thereby maintaining diversity.

Global change effects: from species to communities

Persistence, physiology, geographic range and phenology of species are changing because of global change. Communities are susceptible to be affected by these species' responses to global change due to changes in species composition (nodes of the networks), because of

species extinctions, species invasions or variation in species abundances. In addition, communities can be affected by these species' responses to global change through changes in interactions among species (links of the networks), because of a modification of interaction strengths, a break of existing interactions or emergence of new interactions. However, few empirical studies have focused on this question, our knowledge on the topic remaining mainly theoretical. Here, I will briefly review studies integrating species responses to global change in a community framework, focusing on geographic range and phenological shifts and not considering physiological responses that imply very different approaches.

Spatial and temporal mismatches between interacting species

Since species are moving in space and time and that those responses can vary in direction and strength (Parmesan 2007; Lenoir *et al.* 2020), interacting species might no longer co-occur in space and time, leading to spatial and temporal mismatch respectively. Evidence for temporal mismatch among trophic levels have been accumulated, trophic levels shifting their phenology with different strengths, higher trophic levels advancing less their phenology than lower ones (Thackeray *et al.* 2016). The most documented example is the increasing temporal mismatch between the peak of caterpillar abundance and the peak of nestling demand of birds, a recent review showing that, although birds respond adaptively in time, they fail to follow the advance of the caterpillar peak (Radchuk *et al.* 2019). Such temporal mismatch among interacting species is also occurring in marine ecosystems (Edwards & Richardson 2004), between insect egg hatching and plant bud burst (Visser & Both 2005; Asch *et al.* 2013), between herbivore mammals and plant growth (Post & Forchhammer 2008), flowering periods and pollinator activity periods (Burkle *et al.* 2013; Schmidt *et al.* 2016), etc.. Such mismatches even happen within species, as for example the phenological mismatch occurring between males and females of squirrels in their hibernation phenology, leading to a delay of the reproduction (Williams *et al.* 2017). Although there is no evidence that geographic range shifts differ among trophic levels, interspecific variations can also induce spatial mismatch, similarly to phenological shifts. However, most of the literature considers future projections of spatial mismatch, which I do not consider here, and very few empirical studies based on historical data show that those spatial mismatches among interacting species are currently occurring (Grunsven *et al.* 2007; Zang *et al.* 2020). Understanding the response to climate change of communities from past to present is however the first step to predict the future.

On the need to consider the heterogeneity of species responses

Many studies focus on average mismatch among functional or taxonomical groups of species, neglecting the substantial variation of responses among species within these groups. Such variation can lead to important interaction mismatches, even when the functional groups that interact are on average responding with the same direction and strength to global change. For instance, a species interacting with several species not shifting in space/time with the same direction or strength will be unable to follow all its partners (Memmott *et al.* 2007). This overlooked variance is also key to understand how species responses combine to affect the seasonal structure of communities. Few empirical studies have indeed shown that the seasonal structure of given functional groups was strongly modified because of heterogeneous phenological shifts (Diez *et al.* 2012; CaraDonna *et al.* 2014; Theobald *et al.* 2017; Carter *et al.* 2018; Hällfors *et al.* 2020). Not only phenological shifts can vary among species, thus affecting the structure of communities, but species phenological shifts can also vary over space, leading to the fact that similar communities at different locations can exhibit very distinct changes in their seasonal structure (**Figure I-5**). Changes in the seasonal structure of ecological communities affect the overall structure of the networks, which is likely to affect their stability and robustness to perturbations, stressing the need to investigate how changes in the seasonal structure of a community, a multi-dimensional object, affect community diversity, stability and functioning.

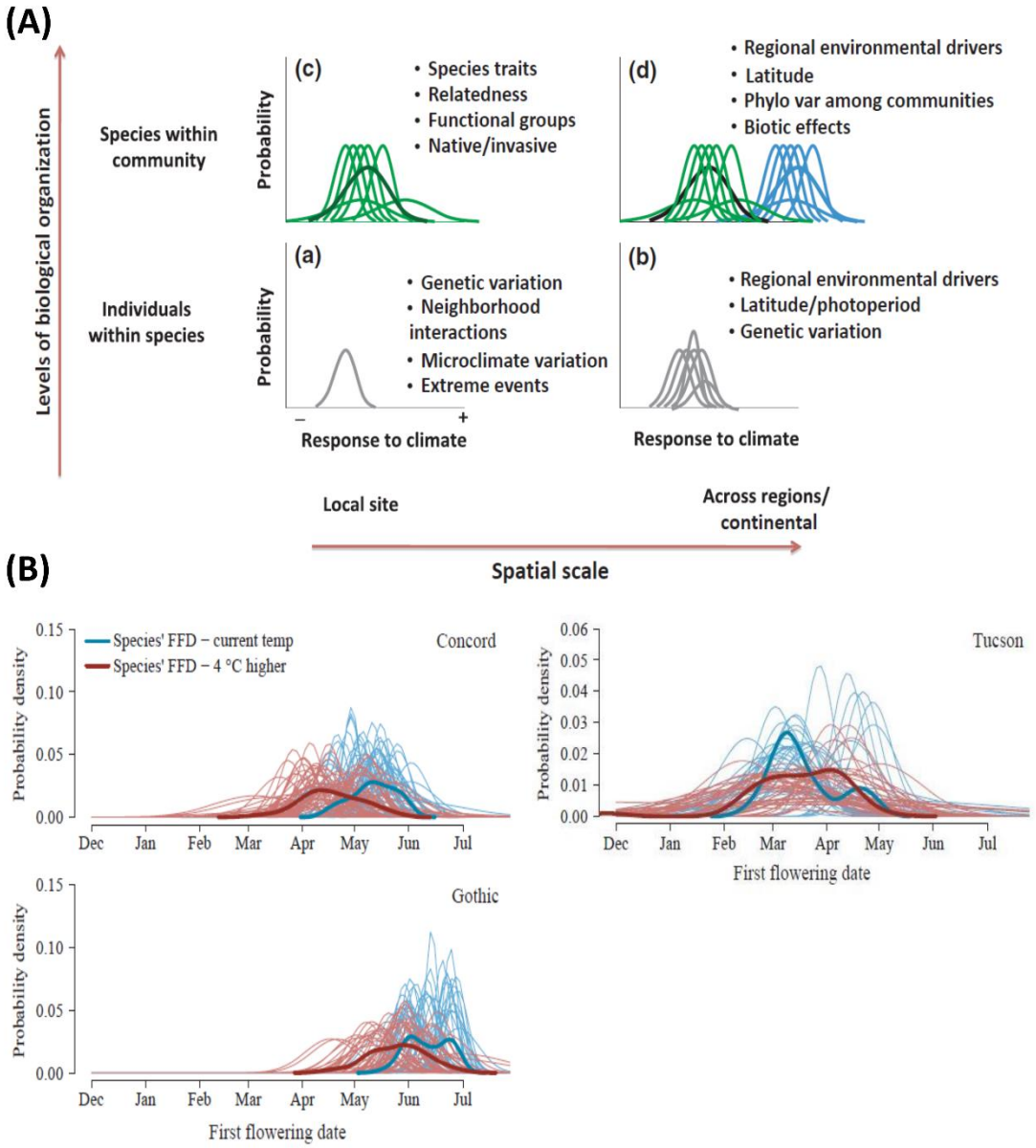

Figure I-5: ***(A) Conceptual diagram showing variability in species phenological responses to climate at different levels of organisation and spatial scales.*** *Hypotheses proposed to explain variation in phenological responses are relevant at different spatial scales (x-axis) and levels of biological organisation (y-axis). Individual curves represent the variation in responses to climate. Phenological responses to climate may vary among individuals within a population (a), among populations across a wider geographic area (b), among species within a particular local community (c) and among communities across a wider geographic scale (d). The dark lines in (c) and (d) represent overall community-level responses.* ***(B) Forecasting expected changes in First Flowering Date (FFD) of three plant communities, using relationships with temperature.*** *Curves represent posterior predictive probabilities of FFD on given dates for each species. Darker, thicker lines represent the seasonal structure (i.e. the overall community-level distributions of dates). Predictions of the FFD for species were made at mean temperatures (blue curves) during the key months and a 4 °C increase in temperature at each site (red curves). Both are extracted from Diez et al. (2012).*

Perturbation propagations through indirect effects

Except in very well studied systems, such as caterpillar-bird breeding phenology, how temporal/spatial mismatches affect community functioning remains unclear. Some studies show that in diverse communities such mismatch could be buffered by functional redundancy among species (Bartomeus *et al.* 2013). However, by changing the co-occurrence of interacting species over space and time, global change can lead to local/seasonal extinctions which might result in cascades of secondary extinctions. Although understanding how communities are and will be affected by species extinctions due to global change seems an important step, very few studies integrate projected species extinctions in a community framework (Pellissier *et al.* 2013; Hattab *et al.* 2016; Staniczenko *et al.* 2017; Bascompte *et al.* 2019). Regarding mutualistic networks, even if their nested structure increase their robustness to species extinctions, including species extinctions in a community framework provide evidence that secondary extinctions are likely to occur (Memmott *et al.* 2007; Bascompte *et al.* 2019).

The consequences of species extinctions are difficult to predict as they can propagate in ecological communities through interactions, from species to species, thus connecting indirectly all species of the network, if it is not perfectly modular. An indirect effect is the effect of one species to another one occurring through indirect interactions (path of length ≥2, **Figure I-6**), which can link two species without any direct interactions between them. Basically, competition is a famous indirect interaction which connect species through indirect effects, for example between two predators sharing a common prey. Although indirect-effects are often considered only on short paths in small motifs (Levine *et al.* 2017) those indirect effects also occur through long-paths, thereby occurring even among species that do not share any common partner/prey/predator. Indirect-effects often have lower strength than direct effects occurring through direct paths (i.e. paths of length one) because of attenuation along paths. However the numerous number of paths through which indirect effects occur in diverse communities make overall indirect effects at least as important as direct interactions among species (Higashi & Nakajima 1995). Studies on empirical food webs show that indirect effects play a fundamental ecological role (Montoya *et al.* 2009; Salas & Borrett 2011).

In mutualistic networks the balance between competition and facilitation is probably strongly linked to species persistence in mutualistic communities (Bastolla *et al.* 2009) but their study remains mainly limited to indirect effects occurring through short paths (i.e. path of length 2), following classical views of competition and facilitation. Two pioneering studies have

shown that when integrated over all possible paths, indirect effects are a very important determining factor of the evolutionary dynamics of mutualistic networks (Guimarães *et al.* 2017) and of their ecological robustness to extinctions (Pires *et al.* 2020). Some empirical and theoretical studies show that phenological shifts affect species coexistence through changes in competitive interactions (Carter & Rudolf 2019; Rudolf 2019), but understanding the ecological role of indirect effects including long-path ones, and how they are affected by phenological shifts is a current key challenge to assess consequences of species phenological shifts at a community level.

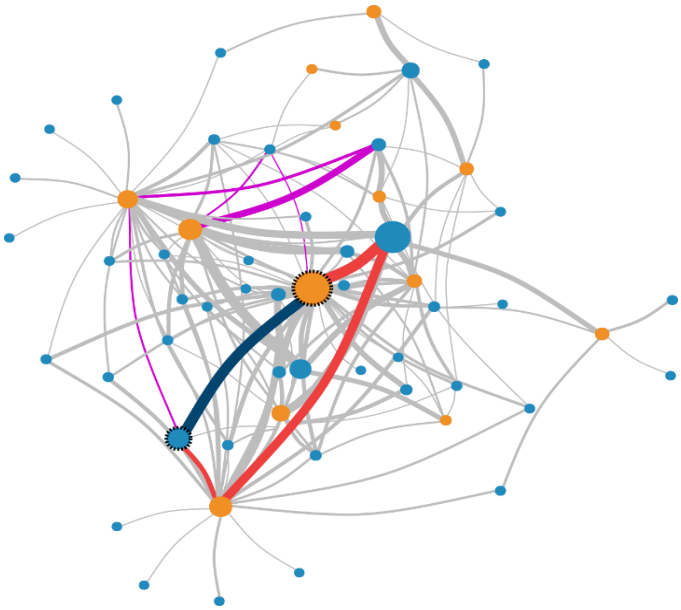

Figure I-6: ***Example of a weighted plant–pollinator network (Memmott 1999).*** *Nodes depict plant (orange) and pollinator (blue) species and lines the interactions between them. The direct path, with length l = 1, between the highlighted species pair is signaled in dark blue, one of the multiple indirect paths with length l = 3 is signaled in red and one of the multiple indirect paths with length l = 5 is signaled in purple. Mofidied from Pires et al. (2020).*

To conclude, while our knowledge on the consequences of geographic range shifts on communities mainly comes from predictive approaches, with very little empirical evidences, some observations have shown that phenological shifts are affecting the seasonal structure of ecological communities. However, we still need to generalize these few results and to link the changes in seasonal structures to community stability and functioning in order to understand how global change affects biodiversity. Moreover, indirect effects seem to play an important role in the seasonal structure of communities (Rudolf 2019) but their role remain widely overlooked, stressing the need to develop approaches focusing on these “invisible” interactions among species.

From communities to species, a neglected eco-evolutionary feedback

Above, we have seen that species responses to global change can strongly change community structure in which they are embedded. However, because species strongly depend on their interspecific interactions (Wisz *et al.* 2013), communities are also likely to affect species responses to global change. First, some studies find strong differences and sometime opposite species responses to environmental changes within or outside of a community context (Davis *et al.* 1998b, a; Suttle *et al.* 2007). This suggests that ecological responses to environmental changes can be affected by inter-specific interactions. Second, the adaptive optimums of geographic range and phenology seem partly driven by inter-specific interactions. For example, the arrival of novel competitors can change spatial/seasonal optimum (Alexander *et al.* 2015; Alexander & Levine 2019; Rudolf 2019). Thus, some authors have proposed that communities are not only affected by species responses, they also drive them (Lenoir *et al.* 2010; Loeuille 2019). This eco-evolutionary feedback from communities to species is often neglected for simplicity while it is probably common, since species are able to develop fast adaptive evolutionary responses to track trophic interactions in the season (Asch *et al.* 2013; Ramakers *et al.* 2019). Indeed, considering that species responses are driven by both abiotic and biotic factors adds a substantial layer of complexity to assess whether shifts in geographic range or phenology are adaptive or not, because their adaptive nature does not depend anymore only on climate. This also adds a conceptual difficulty, as shifts in geographic range and phenology are often viewed as a source of perturbations for communities, and not as an adaptive process driven by communities, making the snake biting its own tail.

Trying to disentangle this loop of feedbacks between species responses and communities is a key challenge to further understand the importance of biotic factors in mediating global change effects on biodiversity. Depending on whether phenological shifts are driven or not by inter-specific interactions, we expect different consequences for communities (Loeuille 2019; Rudolf 2019) as well as depending on whether phenological shifts involve phenotypic plasticity and/or evolution we expect different consequences for species persistence (Chevin *et al.* 2010). Since species do not react in the same way to global change, a strong constraint of inter-specific interactions on species persistence could make impossible for species to track simultaneously biotic and abiotic optimums, possibly increasing species extinctions. If evolution is involved in phenological and geographic range shifts, that opens the door of a putative evolutionary rescue, especially if such evolution allows maintaining species interaction, thereby preventing

community collapse (Loeuille 2019). However, detecting such feedbacks from communities to species responses requires disentangling ecological and evolutionary mechanisms in observed shifts and coupling that with analyses of the changes in community structure, a highly challenging task. Few well studied systems have shown that such evolutionary rescue is occurring to track trophic resources in time, through phenological shifts (Asch *et al.* 2013; Ramakers *et al.* 2019). In addition, pioneering experimental studies over space (Alexander *et al.* 2015) and time (Alexander & Levine 2019; Carter & Rudolf 2019), have shown that effects of shifts in geographic range and phenology on species persistence are strongly mediated by competition among species, suggesting that competition could drive temporal or spatial evolutionary responses. This stresses the need to develop further studies on empirical evidence in un-manipulated systems at large spatial scales to generalize such results.

Knowledge gaps and thesis questions

From the knowledge background about how species respond to global change, especially to climate change, and how these responses are embedded in a community framework, we can identify key issues on which our knowledge remains limited, for several reasons: lack of data, lack of appropriate methods, barely emerging concerns, etc. Below, I present some of these knowledge gaps, which I tried to address in this PhD.

Characterizing species responses to global change drivers

- **How are species responding to global change over space and time? What is the response heterogeneity among species?**

First, studying global change effects on biodiversity needs to describe species responses to global change drivers. The main difficulties in such exercise is the absence of long-term protocoled datasets for many taxa, leading to a lack of baseline reference anterior to the quick global change that has occurred during the last decades (Mihoub *et al.* 2017). To overcome such difficulties, many studies use spatial comparisons among areas with distinct levels of disturbance (Pickett 1989; Winfree *et al.* 2009), substituting time by space to infer species responses to global change drivers. However, space-for-time substitution often neglects local adaptation and site history, which can lead to opposite trends in spatial and temporal patterns

(White & Kerr 2006; Adler & Levine 2007; Isaac *et al.* 2011), highlighting the importance to study temporal series (Dornelas Maria *et al.* 2013).

One potential source of long time series of data for taxa without long-term monitoring schemes are museum and private collections (Bartomeus *et al.* 2019). Although these data are not protocoled and possibly biased in many ways, it has been shown that they allow good estimations of phenological shifts (Loiselle *et al.* 2008; Robbirt *et al.* 2011; Hassall *et al.* 2017) and geographic range shifts of common species (Bates *et al.* 2015). In addition, when analyzed with relevant statistical methods, these data can allow to estimate occupancy trends (Isaac *et al.* 2014; Outhwaite *et al.* 2019; Powney *et al.* 2019), a proxy of species persistence (He & Gaston 2003). Thus, thanks to publicly open databases, the increasing availability of such non-protocoled data, henceforth opportunistic data, opens a new door to estimate species responses to global change over time. Such approach allows estimating temporal species responses at large spatial scales and with a relatively good historical depth, providing "pre-global change" baselines.

- **What is the relative contribution of different global change drivers in different species responses?**

Second, as several global change variables can drive species responses over time, to further understand what is affecting biodiversity we need to develop studies simultaneously assessing the relative role of global change drivers on different species responses. These relative contributions of global change drivers can be difficult to identify because several drivers might exhibit correlated temporal trends and nonetheless have an impact on species responses. We thus need to develop approaches allowing to break correlations among drivers to estimate their relative role in biodiversity changes, in order to properly target conservation measures.

- **What are the eco-evolutionary mechanisms driving phenological shifts?**

Third, understanding how global change is affecting evolutionary trajectories of species requires to assess the eco-evolutionary mechanisms, phenotypic plasticity vs evolution, underlying observed shifts. The "problem of estimating the relative roles of evolution and plasticity is tractable with extensive, long-term ecological and genetic data" (Parmesan 2006) but those are also missing for many taxa. Indeed, current tests for micro-evolutionary changes are very costly in terms of time, human and financial resources, as they request long-term datasets of monitored populations (Charmantier & Gienapp 2014; Merilä & Hendry 2014).

Overcoming such limits in studying past responses to global change would require to develop statistical approaches estimating the contributions of phenotypic plasticity and evolution in observed shifts over time, similarly to what was done to assess phenotypic plasticity and local adaptation over space (Phillimore et al. 2010; Roy et al. 2015). Although such approaches have deep limits that seem unbreakable, for many taxa they are the only way to investigate the mechanisms underlying observed shifts since we cannot turn back the clock to monitor past populations.

Integrating species responses in a community framework

- **How species responses to global change combine to affect the seasonal structure of communities? Do these consequences at community level vary over space?**

The main difficulty to study how species responses affect communities is mainly due to the fact that species responses are often only described for a small number of species over limited temporal and spatial scales, due to limits cited above. This prevents from assessing consequences at a community level because this requires: (i) to assess species response(s) to global change for numerous species to get a representative sample of species belonging to the given community, (ii) to generalize these results by studying spatial variations among species responses and consequences at the community levels. Furthermore, as different species responses (e.g. phenological shifts and abundance trends) can combine themselves and have synergistic effects on community structure, we also need to develop studies combining different drivers of global change to fully understand consequences of multiple species responses at a community level.

- **What is the importance of the seasonal structure in communities? Are the communities robust to changes in this seasonal structure ?**

Furthermore, once the limits stated above have been overcome, we need to link changes in the seasonal structure of communities to the functioning and temporal dynamics of communities, to understand whether such changes at the community level are likely to affect ecological functions and services or not. To do so we need to estimate the functional changes associated with species responses to global change in empirical communities. We also need to develop theoretical models to understand how the seasonal structure affects community diversity and stability. Once merged together, those studies should give us better knowledge on

how changes in the seasonal structure of communities will also affect community diversity and functioning.

- **What is the importance of inter-specific interactions in driving species responses to climate change over space and time?**

Finally, understanding the eco-evolutionary feedbacks between species responses and community structure is a key challenge to understand if communities are undergoing species responses and/or if they drive them. Disentangling this feedback loop would allow to further understand if biodiversity changes can be buffered by evolutionary rescue or not but it is a challenging task. To do so, we need first to disentangle ecological and evolutionary responses, phenotypic plasticity *vs* evolution, in observed shifts. Second, we need to link mechanisms of observed shifts, phenotypic plasticity *vs* evolution, with putative changes in the community structure. For the first (Phillimore *et al.* 2010; Asch *et al.* 2013; Roy *et al.* 2015) and the second (Diez *et al.* 2012; Carter *et al.* 2018) points some studies showed the way forward, and could allow us to investigate this issue further once merged together.

This PhD aims to try to start answering the questions highlighted above, using a famous study model: plant-pollinator communities and the associated pollination function. Since joint datasets of plants and pollinators are almost non-existent at large spatial and temporal scales, we addressed these questions using either pollinator or plant assemblages, finally merging both species assemblages using theoretical approaches. In the following parts, I summarize the methods used to answer these questions as well as the obtained results, before discussing them.

II. Methods & Results

This part is a brief presentation of some main results of my PhD, extracted from six projects of articles conducted during these three years, listed below. A complete presentation of methods, results and figures is thus available in articles/drafts, which are in **Annexes**.

- Duchenne F., Thébault E., Michez D., Elias M., Persson M., Rousseau-Piot J. S., Pollet M., Vanormelingen P. & Fontaine C. Phenological shifts alter the seasonal structure of pollinator assemblages in Europe. *Nat. Ecol. Evol.* **4**, 115–121 (2020). https://doi.org/10.1038/s41559-019-1062-4 (**Appendix I**)
- Duchenne F., Thébault E., Michez D., Gérard M., Devaux C., Rasmont P., Vereecken N. J. & Fontaine C. Long-term effects of global change on occupancy and flight period of wild bees in Belgium. *Accepted in Global Change Biology* (**Appendix II**)
- Duchenne F., Martin G. & Porcher E. Not always a debt: northern cost but southern benefit for European plants lagging behind climate. *In review in Ecology Letters* (**Appendix III**)
- Duchenne F., Fontaine C., Teulière E. & Thébault E. Phenological traits increase persistence of mutualistic networks and promote positive indirect effects. *In prep.* (**Appendix IV**)
- Duchenne F., Thébault E & Fontaine C. Disentangle phenotypic plasticity and evolution in phenotypic shifts: is competition driving pollinator flight period shifts? *In prep.* (**Appendix V**)
- Duchenne F., Fontaine C. & Thébault E. The robustness of pollination networks to phenological shifts depends on competition and diversity. *In prep.* (**Appendix VI**)

Assessing species responses to global change

Since this PhD investigates how global change affects biodiversity over time, the first challenge was to assess the effect of global change on species. Although species is just an arbitrary classification level of life kingdom, it often allows discretizing the diversity of living forms in a manageable number of monophyletic boxes, neither too wide nor too narrow, making it possible to apprehend the diversity of the Eukaryotes, as it is often much less useful for Prokaryotes. Since here we worked on animals and plants, we considered species as the elementary blocks of ecological systems. Assembling these elementary blocks to study upper levels of organization, such as community requires to characterize the spatial and inter-specific variations of species responses to global change in time. To do so, we needed datasets at wide spatial scales, country or continental scale, including a wide diversity of species. Most importantly, as global change has strongly accelerated in the second part of the 20th century

(Steffen *et al.* 2006), we needed a dataset allowing to "go back in time" to about 1950, to study species responses on temporal scales relevant to global change.

Since long-term protocoled datasets are very scarce for insects and plants and remain limited to few taxa or habitats, we used opportunistic datasets to characterize species responses to global change. Those datasets include historical records from museum and private collections as well as recent records from citizen sciences and open monitoring schemes (**Figure II-1**).

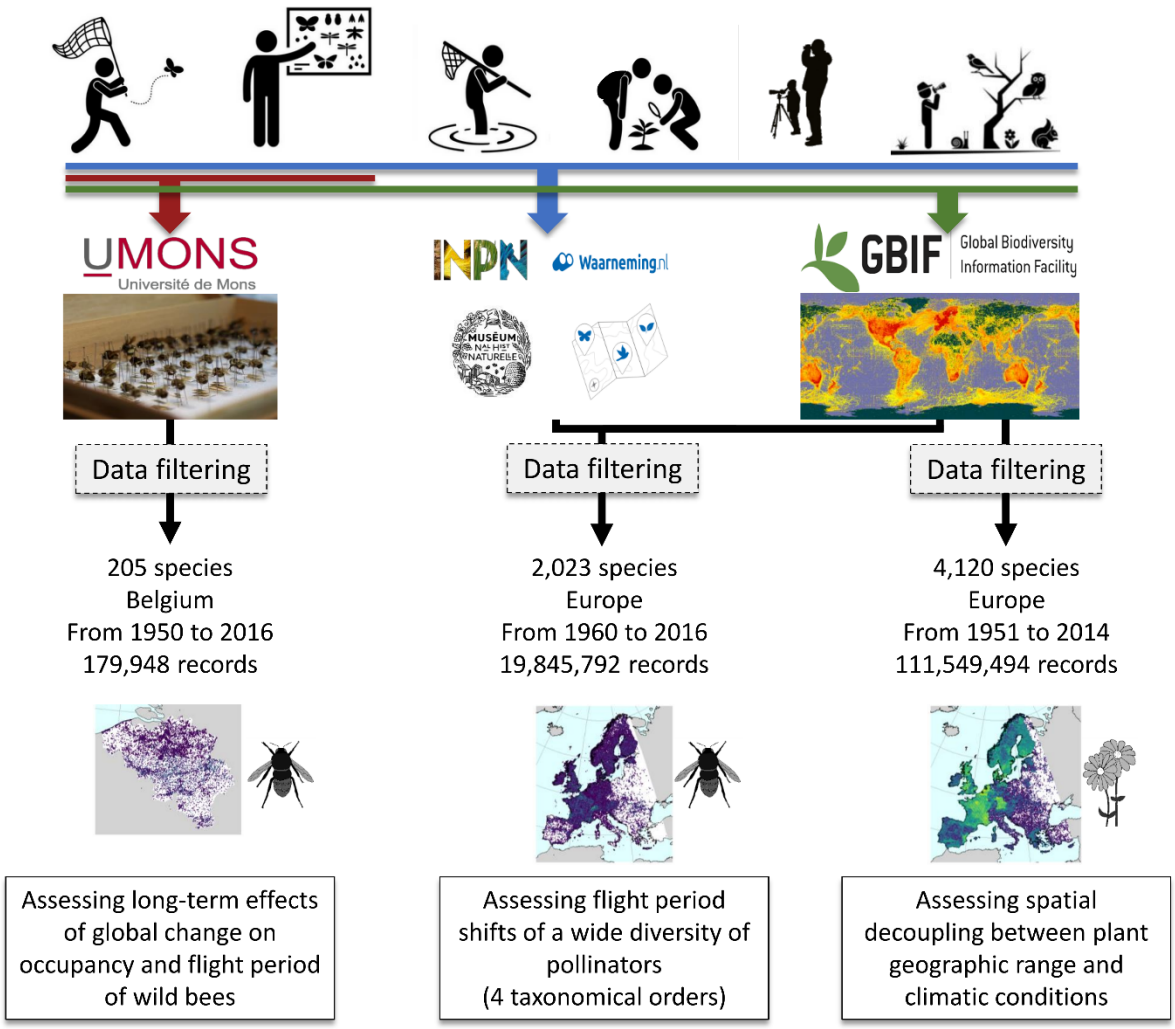

Figure II-1: *Datasets used to characterize species responses to global change. Pictograms at the top show different kind of collection processes used by data providers, from historical naturalist practices (right) to modern citizen sciences (left). Picture credit: Matthew W. Austin.*

Using these datasets, we assessed three distinctive kinds of species temporal responses to global change: pollinator phenological shifts, spatial (de)coupling between climatic conditions and plant distributions, and plant and pollinator occupancy trends. Since we worked with opportunistic data, we had to address putative issues due their non-protocoled side and tried to correct most important biases among the numerous putative ones. Here, we mainly followed guidelines derived from previous studies, which have shown that such data can provide unbiased estimate of phenological events once accounted for location of observations when studying average dates only (Robbirt *et al.* 2011; Bishop *et al.* 2013a; Hassall *et al.* 2017; Bartomeus *et al.* 2019), and relatively good estimates of the climatic conditions experienced by species throughout their geographic range (Tiago *et al.* 2017; Pender *et al.* 2019). In contrast, jointly estimating changes in average date of an event and changes in event duration requires more complex methods. Similarly, estimating occupancy probabilities from such kind of data is challenging because it requires to account for sampling pressure and eventually for changing detection probability (Isaac *et al.* 2014). Consequently, we used basic methods to estimate changes in average climatic conditions associated with species geographic range and in pollinator mean flight date shifts and a bit more complex models to jointly estimate changes in average date and length of pollinator flight period and to estimate occupancy trends (**Figure II-2**).

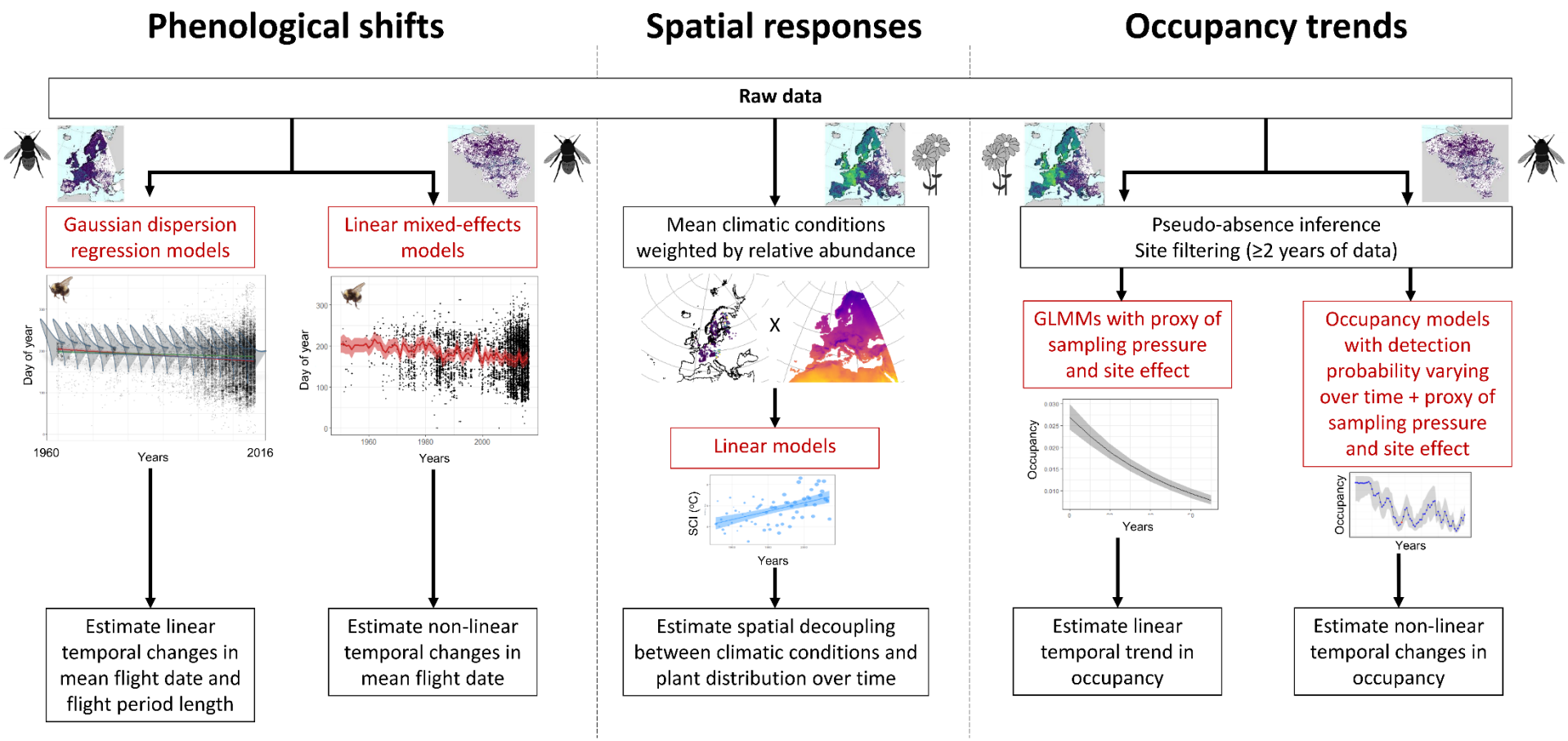

Figure II-2: *Overview of methods used to characterize species responses over time. Maps and pictograms refer to datasets presented in* ***Figure II-1****.Red boxes represent statistical steps, while bottom boxes represent final goals. GLMM stands for Generalized linear mixed-effect model. Proxy of sampling pressure is the logarithm of the number of species detected, based on the known relationship between sampling pressure and species richness.*

Modelling pollination networks with a seasonal structure

While species responses to global change can be assessed over time for each guild of pollination networks, plant and pollinators, datasets gathering historical information about plant-pollinator interaction networks are nonexistent. Consequently, because studying empirically consequences of species responses to global change on plant-pollinator interactions is not possible, we shifted to theoretical models to investigate these questions. Also because it is fun, but unfortunately the pleasure of doing things does not appear as a good enough justification for serious people. That explains why I constantly justify the interest of projects with various arguments, whereas fun was actually the real reason for having done them[6].

Our model describes the mutualistic interactions between two guilds, pollinators (P) and flowers (F), but including competition for partners among species belonging to the same guild (**Figure II-3a**). Mutualistic interactions are obligate and defined by a two-dimensional trait matching between plant and pollinators, involving phenological and morphological matches. In concrete terms, we modeled temporal variations of abundance of n_p species of pollinators and n_f species of flowering plants belonging to the same community, by using one differential equation by species. Since many theoretical tools are based on equilibrium conditions, we solved the system numerically until we reached an equilibrium (i.e. stationary abundances, **Figure II-3b**), allowing us to study network properties First, we studied the importance of the seasonal structure in maintaining diversity in pollination networks by considering the balance between positive and negative direct and indirect effects. To estimate the relative strengths of direct and indirect effects among pairs of species, we used a method based on the interaction coefficients contained in the Jacobian matrix (Nakajima & Higashi 1995). By direct effects we considered here mutualistic interaction among guilds and competition within guilds, implemented as a direct effect. By indirect effects we consider the overall sum of all effects occurring through paths of length ≥ 2 **Figure II-3c**). Second, we applied phenological shifts during 60 years before phenologies were stabilized, and we waited until the system reached a new equilibrium. By comparing equilibriums before and after phenological shits we measured the robustness of pollination networks to phenological shifts and its determining factors.

[6] « *Le savant n'étudie pas la nature parce que cela est utile ; il l'étudie parce qu'il y prend plaisir et il y prend plaisir parce qu'elle est belle.* » Henri Poincaré, *Science et méthode* (1908)

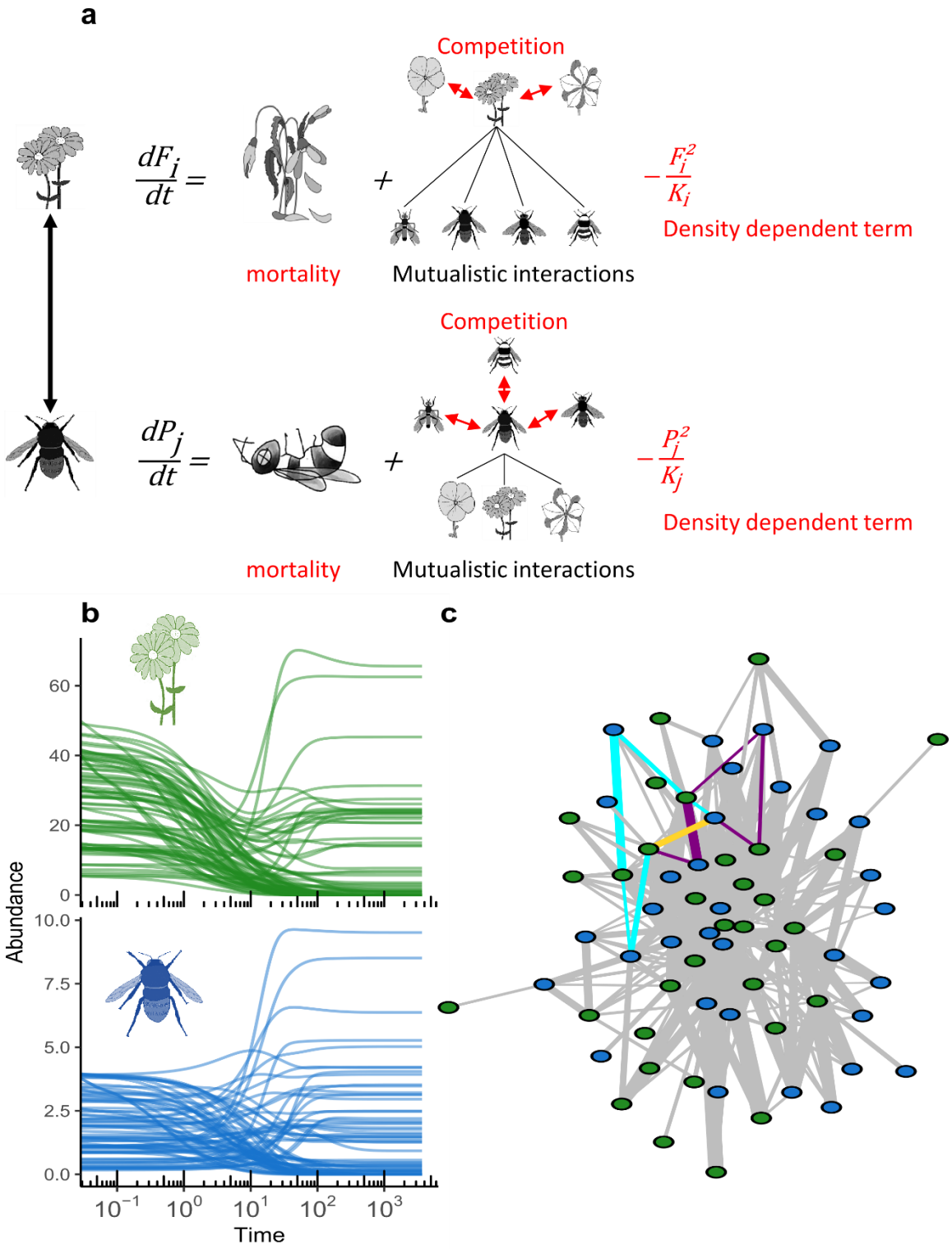

Figure II-3: ***Schematic presentation of the theoretical model developed here.*** *(a) Schematic view of the differential equations used for each species of plants and pollinators. (b) An exemple of simulation showing how species abundances vary in time before reaching a stationary state. (c) An example of plant-pollinator interaction networks at equilibrium, green dots represent plant species, blue dots the pollinator species while grey links represent the weighted interactions. The yellow link represents an exemple of a direct interaction between a plant and a pollinator (path of length = 1), that can also be linked through indirect paths (of lengths ≥1). Two examples of such indirect paths of length = 5 are shown in light blue and purple.*

Changes in the seasonal structure of pollinator assemblages

Pollinators play an important role in terrestrial ecosystems by providing key ecosystem functions and services to wild plants and crops, respectively. The sustainable provision of such ecosystem functions and services requires diverse pollinator communities over the season. Despite evidence that climate warming shifts pollinator phenology, a general assessment of these shifts and their consequences on pollinator assemblages is still lacking. In the first project (cf. **Appendix I**), by analyzing phenological shifts of over 2000 species, we showed that on average the mean flight date of European pollinators shifted 6 days earlier over the last 60 years, while their flight period length decreased by 2 days. We highlighted that phenological shifts exhibit a strong variation among species, which is seasonally, spatially and phylogenetically structured. Our analysis further revealed that these shifts have likely altered the seasonal distribution of pollination function and services by decreasing overlap among pollinators' phenologies within European assemblages, except in the most northeastern part of Europe (**Figure II-4(A)**). Such changes are expected to decrease the functional redundancy and complementarity of pollinator assemblages and as such, might alter the performance of pollination function and services and their robustness to ongoing pollinator extinctions. From this analysis, we also showed that it is preferable to check the spelling of the names of the co-authors before publication (cf. **Appendix Ibis**).

Global change affects species not only by modifying their activity period but also their abundance. The challenge is now to identify the respective drivers of those responses and to understand how those responses combine to affect species assemblages and ecosystem functioning. In the second project of this PhD (cf. **Appendix II**) we correlated changes in occupancy and mean flight date of 205 wild bee species in Belgium with temporal changes in temperature trend and inter-annual variation, agricultural intensification and urbanization. Over the last 70 years, bee occupancy decreased on average by 33%, most likely because of agricultural intensification, and flight period of bees advanced on average by 4 days, most likely because of inter-annual temperature changes. Heterogeneity in occupancy trends were strongly linked to bee size and sociality, consistently with a decline that could be driven by habitat fragmentation and pesticides, while heterogeneity in phenological shifts were related to climatic niche and sociality. We found a weak but significant correlation between species responses, without being able to interpret the causal links among both responses. Phenological shifts and changes in occupancy resulted in a synergistic effect between occupancy and flight period shifts

because species which increased in occupancy tended to be those that have shifted their phenologies earlier in the season. This led to an overall advancement and shortening of the pollination season by 9 days and 15 days respectively, with lower species richness and abundance compared to historical pollinator assemblages, except at the early start of the season (**Figure II-4(B)**). Our results thus suggest a strong decline in pollination function and services.

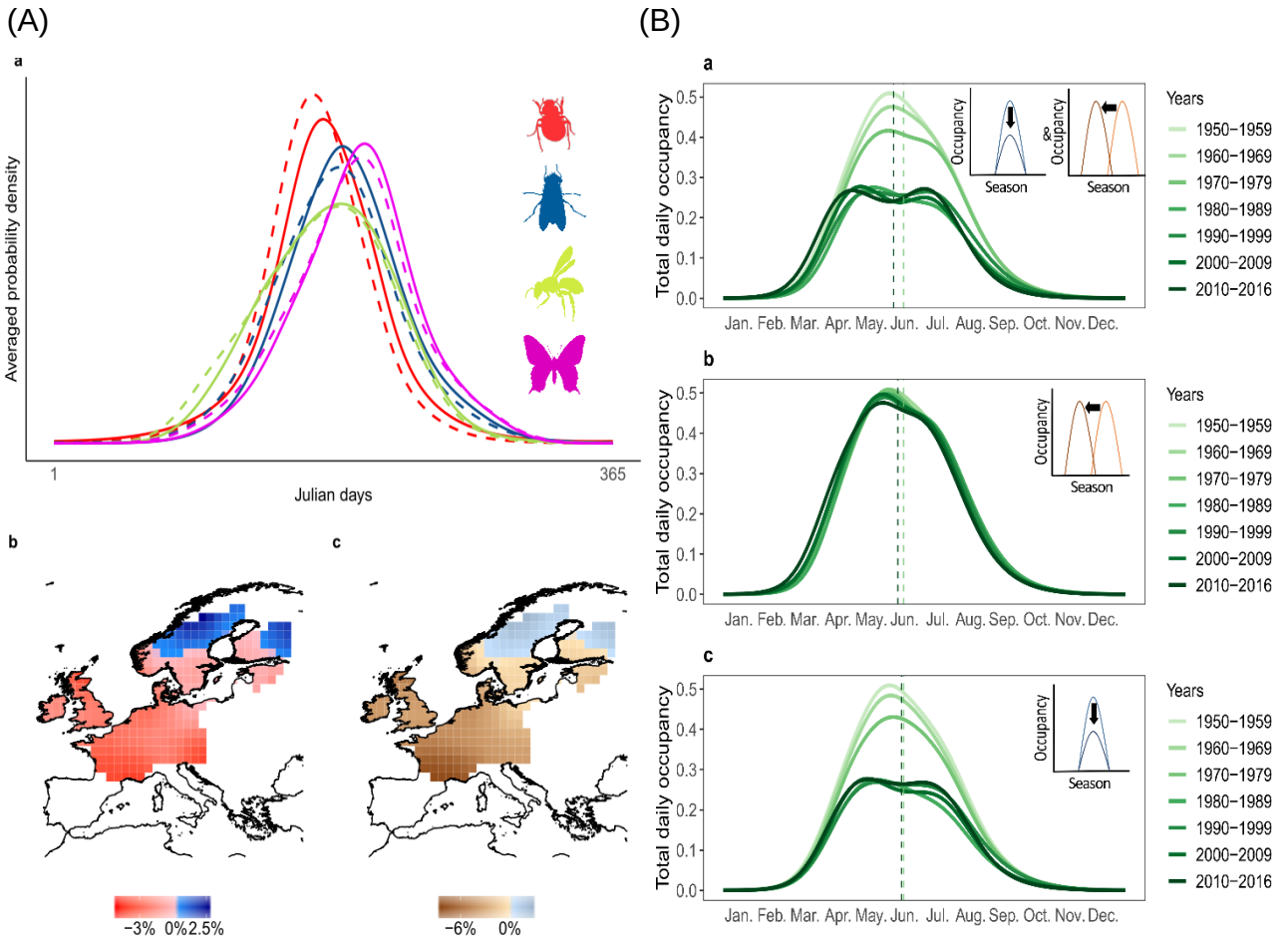

Figure II-4:* (A) Changes in within- and among-orders average overlaps in phenology between 1980 and 2016 across Europe.** *(a) Average phenology over all species in 1980 (solid lines) and in 2016 (dashed lines) for one grid cell (centroid = 55,0) by orders: Coleoptera (red), Diptera (blue), Hymenoptera (light green) and Lepidoptera (magenta). The average phenology is calculated by averaging all probability density functions (Gaussians representing phenologies) over all species of each orders, assuming identical species abundances. Observed changes in the average overlap among phenologies between 1980 and 2016, within orders (b) and among orders (c). Uncolored cells are under-prospected.* ***(B) Seasonal variations of the total occupancy of pollinators over decades. *(a) Reconstruction considering both occupancy and MFD changes, (b) reconstruction considering only MFD shifts, historical occupancy being fixed over decades, and (c) reconstruction considering only occupancy changes, historical MFD being fixed over decades. Dashed vertical lines represent the weighted mean of the seasonal total occupancy distribution for 1950-1959 (light green) and for 2010-2016 (dark green).*

Geographic range shifts are linked to species persistence

In addition to moving in time, species can also track their ecological optima by moving in space. For many species, climate change leads to detectable, but often insufficient, range shifts. Such lag of species range shifts behind climatic conditions is often coined a "climatic debt", but its demographic costs have never been evaluated. In the third part of this PhD project (cf. **Appendix III**), we jointly assessed temporal shifts in climatic conditions experienced by species and species occupancy trends, for about 4,000 European plant species over the last 65 years. By showing that plants that are lagging behind climate change are also the one that decrease the most, we provided the first piece of evidence that European plants are already paying a climatic debt in Alpine, Atlantic and Boreal regions. In contrast plants lagging behind climate change benefit from a surprising "climatic bonus" in the Mediterranean (**Figure II-5**), likely temporary and might be mediated by changes in competition pressures. We also found that among multiple pressures faced by plants, climate change is now on par with other known drivers of occupancy trends, such as eutrophication and urbanization.

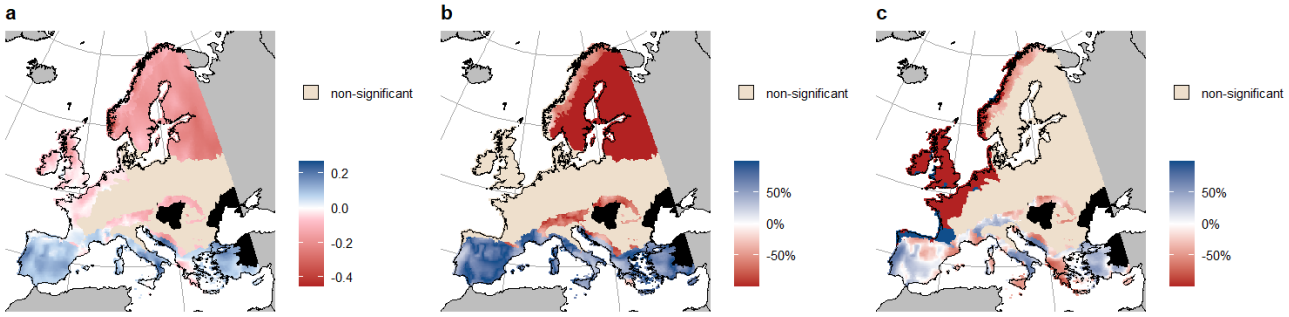

***Figure II-5:* Climatic debt/bonus in Europe and its climatic drivers.** *(a) Climatic debt/bonus averaged over all species over the last 65 years. The gradient from white to red indicates a climatic debt (cost of climate change in terms of species occupancy), while the gradient from white to blue indicates a climatic bonus (benefits of climate change in terms of species occupancy); white represents no cost of range shift lags on average for plants. Relative contribution of (b) temperature and (c) precipitation SCI trends to the climatic debt/bonus, in percentage. Black regions are biogeographic regions with too few data.*

Eco-evolutionary mechanisms of phenological shifts

Increasing evidence shows that climate change affects numerous species phenotypic traits, such as the seasonal timing of biological events. However, the underlying mechanisms of these phenotypic changes, such as abiotic *vs* biotic factors or phenotypic plasticity *vs* evolution,

remain widely overlook because it requires time consuming and costly population monitoring, while it is key to understand how climate change affects evolutionary trajectories of species. In the third project of this PhD (cf. **Appendix IV**), we proposed to use a statistical partitioning of phenotypic plasticity and evolution of phenotypic shifts, using historical data without any information about pedigree or fitness that are commonly used to do so. Using simulations and a known case study on bird breeding phenology, we showed that our method gives consistent estimate of phenotypic plasticity and evolution. Studying pollinator flight period shifts in Great Britain, we found that their long-term shifts in mean flight date are likely driven by evolution rather than by phenotypic plasticity to temperature. Moreover, by integrating these changes in flight periods at a community level, we showed that the evolution of mean flight dates might be driven by competition pressures. Such results echo theoretical ones and provide new elements to understand what mediates species responses to global change.

Consequences of species phenologies in a community framework

Results presented above show that the seasonal structure of pollinator assemblages is changing over years, because of a synergistic effect of flight period shifts and pollinator decline. However, the links between this seasonal structure and community persistence remain widely overlooked, as most of the theoretical and empirical studies aggregated ecological networks over time. However, few studies have focused on the seasonal dynamics of plant-pollinator interactions and showed that phenological and morphological traits play an important role in structuring pollination networks (Junker *et al.* 2013; CaraDonna *et al.* 2017; Manincor *et al.* 2020; Peralta *et al.* 2020). These two kinds of traits involve distinct mechanisms, phenological traits decouple interactions in time while morphological traits mainly create forbidden links. While these differences are likely to affect the indirect effects among species and thus network persistence, it remains an overlooked side of ecological networks. In our first project (cf. **Appendix V**), using dynamic models we focused on how phenological and morphological forcings (i.e. the strength of the niche partitioning due to the phenological and morphological traits respectively) drive community persistence and affect indirect effect strengths. Our results show that within guilds, the relative importance of positive indirect effects – when compared to competition – is stronger in network structured by phenological traits than in those structured by morphological traits, increasing network persistence (**Figure II-6**). This buffering of competition by phenological traits allows maintaining specialists, the most vulnerable species,

which propagate the most positive effects within guilds and promote nestedness. Our results underlie the role of the kind of traits structuring ecological networks, and highlight the important role of the phenology in communities.

Then, to investigate how global change can affect plant-pollinator interaction networks through species responses, we used this dynamic model to assess the robustness of plant-pollinator interaction to phenological shifts (cf. **Appendix VI**). We applied different kinds of phenological shifts, varying independently the heterogeneity in phenological shifts among species and the average mismatch in phenological shifts between plant and pollinator guilds. We showed that competition strength decreases the robustness of pollination network to phenological mismatch between plant and pollinator and to heterogeneous phenological shifts, both types of phenological shifts equally affecting pollination networks. High diversity and short pollination season length buffer the negative effect of heterogeneous phenological shifts but not of average plant-pollinator mismatch. In addition, we showed that although a decrease of the strength of mutualistic interactions is the main driver of species decline, changes in competition pressures play a non-negligible role in abundance changes because of phenological shifts, while it is widely overlooked in mutualistic networks. Our results highlight a positive diversity-stability relationship, raising concerns that pollinator decline act synergistically with the ongoing phenological shifts, leading to negative consequences on pollination functions and services.

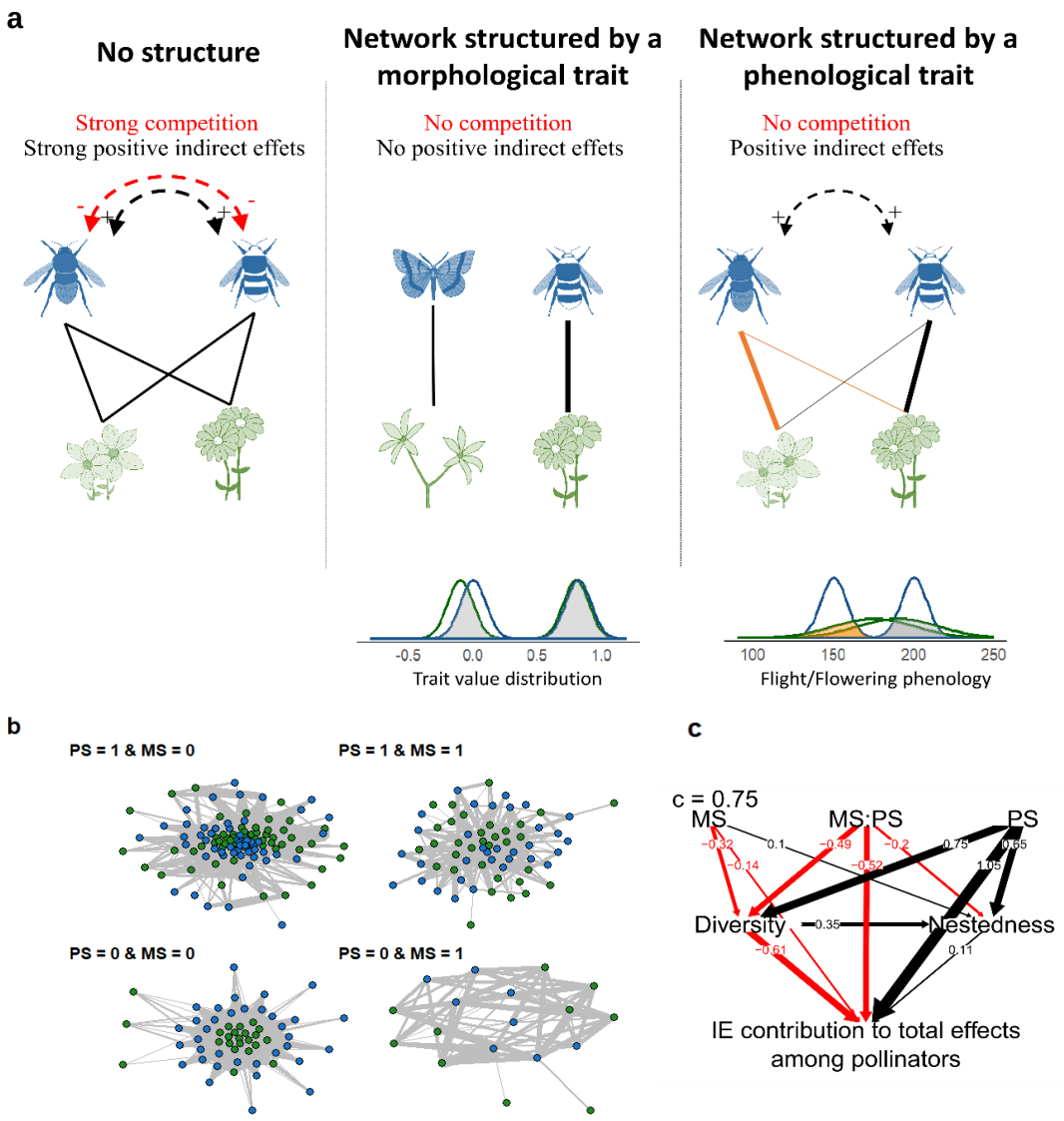

Figure II-6: ***Theoretical mutualistic networks structured by different kinds of traits, and indirect effects strength.*** *(a) a small pollination network without any structure (left), structured by a morphological trait (middle) or by a phenological trait (right) to remove competition. Links represent mutualistic interactions (+/+) whereas indirect effects among pollinator are represented by dashed arrows. Gaussians represent the trait value distribution or the flowering/flight period for plants (green) and pollinators (blue), and the overlap among them (colored area) representing the interaction strength. (b) Example of networks at equilibrium for extreme values of phenological forcing (PS) and morphological forcing (MS) and for a given value of intra-guild competition (c = 0.5). Network was constructed by multiplying interaction values by the geometric mean of associated species abundances. Then we simplified the network by removing link with a weight lower than one. Blue points represent pollinators while green points represent plants. (c) relationships among traits, structure, diversity and contribution of indirect effects (IE) to total effects among pollinators. Values on arrows are standardized coefficients of the multi-group path-analysis performed on data for a given value of intra-guild competition strength (c = 0.75). This model includes an interaction (MS:PS) between the phenological (PS) and morphological (MS) forcings. Diversity is the number of persistent species at equilibrium.*

III. Discussion

Together these research projects have shown that species phenology, geographic range and persistence are changing over time because of global change, with consequences for communities. In what follows, I will discuss these findings, highlighting what I see as the most significant results of this PhD, and trying to have a transversal look across papers.

Temporal dynamics of biodiversity

Most of this PhD deals with the temporal dynamics of biological entities, from species to communities, and from long time scales over several decades, to shorter time scales, looking at a season within a single year. Most of my projects even merged these different levels of analyze, studying changes in the seasonal structure over years. In this part, first focus on why the study of long-term time series is necessary to understand how global change affects biodiversity, second develop on the importance to consider the seasonal dynamics of biodiversity.

Long-term temporal dynamics, over years

Space-for-time can be misleading

Because long-term monitoring schemes only exist for a few taxonomical groups, the study of how each global change driver affects biodiversity mainly comes from spatial comparisons among areas with distinct levels of disturbance (Pickett 1989; Winfree *et al.* 2009). However, assessing how global change, a temporal process, affects biodiversity by a space-for-time-substitution can be misleading because it neglects site history, local adaptation and the diffusion of perturbations over habitats and landscapes. Indeed, by neglecting what became extinct because of global change before present, space-for-time substitution approaches are based on a strongly bias sampling of biodiversity, compared to pre-global change reference. Moreover, in western countries, especially in Europe, almost every landscapes and habitats have been affected by recent anthropogenic perturbations, spatial gradients only reflect damaged habitats gradients. Using space-for-time substitution only to infer the effects of global change on biodiversity is similar to studying evolution of the life without considering paleontological records. Those records provide important information about what was present but is no longer

present. Neglecting the cemetery of evolution[7] leads to misunderstanding evolution, and similarly neglecting temporal data in global changes studies leads to misestimate global change effects on biodiversity (**Figure III-1**).

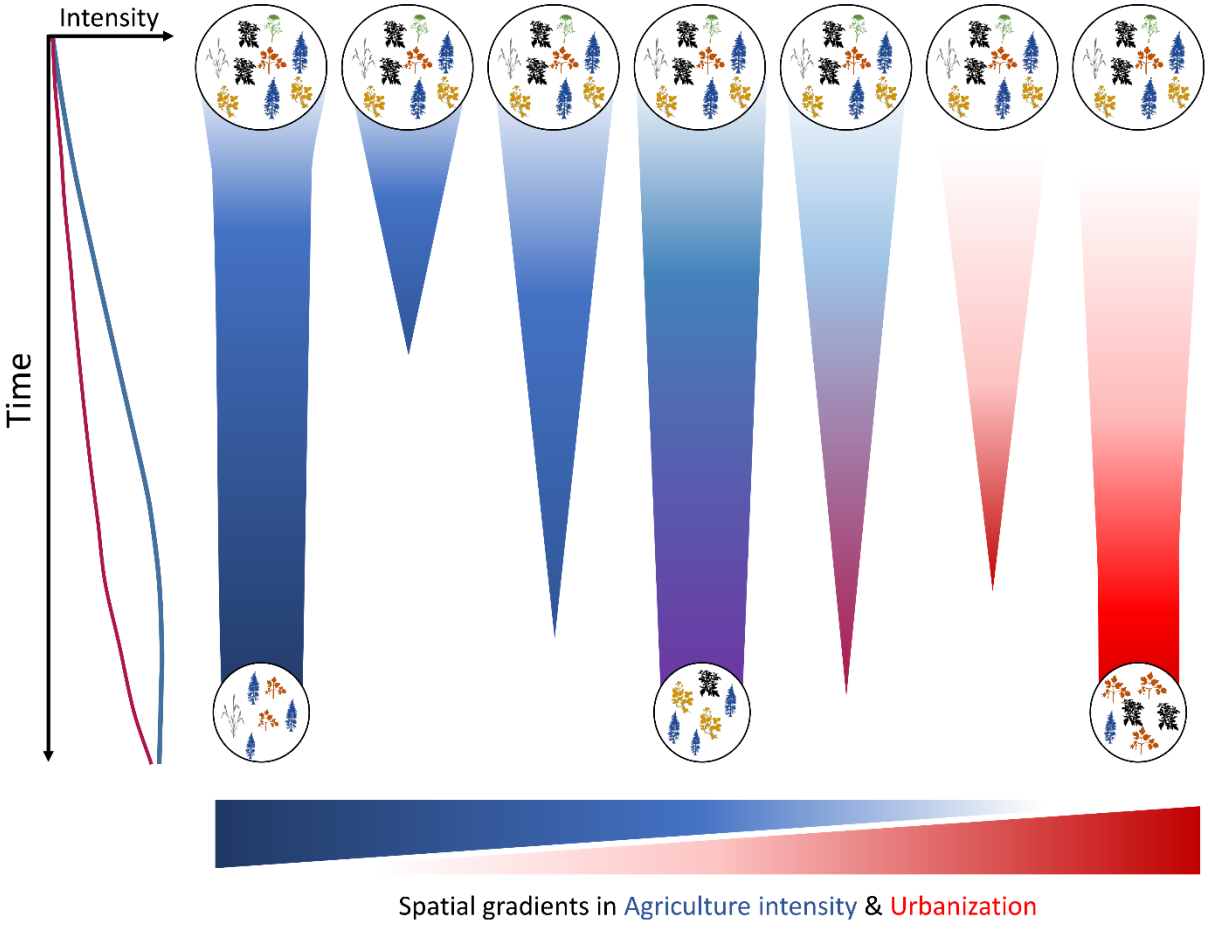

Figure III-1: ***Time series vs space-for-time substitution to infer global change effects on biodiversity.*** *Schematic represenation of the temporal dynamics of an historical homogeneous landscape with 7 identical plant communities under a global change scenario involving agricultural intensification (blue gradient) and urbanization (red gradient). The temporal dynamics of global change drivers are presented on the left, while their spatial gradients are presented at the bottom. The size of the circles is proportional to the community diversity. Four communities collapsed before current time, while three of them persisted. By comparing diversity along the spatial gradients at current time, no signal would be observed because the three communities have the same diversity and because we missed collapsed communities. In contrast studying the system over time would reveal a strong negative effect of agricultural intensity and urbanization on plant diversity.*

[7] "*But just in proportion as this process of extermination has acted on an enormous scale, so must the number of intermediate varieties, which have formerly existed, be truly enormous. Why then is not every geological formation and every stratum full of such intermediate links? Geology assuredly does not reveal any such finely graduated organic chain; and this, perhaps, is the most obvious and serious objection which can be urged against the theory. The explanation lies, as I believe, in the extreme imperfection of the geological record.*" Charles Darwin

In the **Appendix II** we showed that using the dynamic of global change drivers (i.e. the speed of change) instead of their temporal trend allows breaking correlation among drivers and with time. I think that this methodological step was important, because it then allows estimating independent effects of each global change drivers on occupancy or flight period of wild bees, showing that correlations among global change drivers can be overcome when analyzing time series, by focusing on their kinetic rather than on their values. However, the drawback is that such method focuses on immediate responses from species to global change drivers only, neglecting the level of pressure. Thus, further methodological developments are required to account for immediate and time-lagged effects simultaneously.

Short-term time series miss evolutionary responses

However the study of time-series is not sufficient to properly assess the effects of global change on biodiversity, we also need to study long-term time series (Dornelas Maria *et al.* 2013). For example, regarding phenological shifts, many studies assume that phenological shifts are mainly driven by phenotypic plasticity and relate the timing of phenological events to temperature, without accounting for any temporal dimension (Hodgson *et al.* 2011; Diez *et al.* 2012). Using temperature instead of time as a covariate to assess changes in phenologies allows to use short time series, as the inter-annual temperature variations are often important and phenology is very plastic to temperature (Cohen *et al.* 2018). Such approach thus considers only the plastic response to temperature and strongly neglects putative evolutionary responses, possibly leading to misestimate phenological shifts because to climate warming.

By using a statistical partitioning of temperature-correlated and time-correlated effects on mean flight date shifts of pollinators over 1960-2016 in Great-Britain (**Appendix IV**), we found that the phenotypic plasticity of pollinators was indeed very high, and led to an advancement of the mean flight date over time. This is consistent with previous estimations of phenotypic plasticity to temperature in butterflies and flower flies (Roy *et al.* 2015; Hassall *et al.* 2017). However, we also showed that there is a temporal trend in mean flight shifts that is independent from phenotypic plasticity to temperature. This temporal trend tends to buffer the advancement of mean flight date related to plastic response. Although our approach does not allow to infer evolution properly, our time-correlated effect is likely to be a signal of evolution because natural selection works on generations, thereby producing phenotypic changes correlated with time, and because it is independent from phenotypic plasticity to temperature. I think that this

result might explain why predicting phenological shifts through time from the relationship between the timing of phenological events and temperature can bring inaccurate results (Ellwood *et al.* 2012) and echoes theoretical hypothesis that species should evolve to face long-term environmental changes (Visser 2008). Finally, our results highlight the need to study long-term temporal trend from the past to understand species responses to global change, rather than focusing on projecting future changes from short-term studies.

A shifting baseline syndrome?

Finally, in addition to study long-term time series, those time series should allow to estimate changes compared to a baseline which is before the recent acceleration of global change. Because of the fact that the main drivers of biodiversity loss involve fast changes that occurred 50 years ago (**Figure III-2a**), most of the studies focusing on the last decades probably miss an important part of the global change effects on biodiversity potentially leading to a *shifting baseline syndrome* (Pauly 1995; Jackson *et al.* 2001; Knowlton & Jackson 2008). Indeed, because historical biodiversity data are rare, studies mainly focused on recent and short time-series. This implies a recent baseline reference that strongly change the estimated trends. Our results on long-term datasets with a baseline in the 60s allow estimating changes in species occupancies that would have been missed with a baseline in the 80s (**Figure III-2b**). The recent contradiction between studies evidencing a strong decline of insects (Hallmann *et al.* 2017; Powney *et al.* 2019; Seibold *et al.* 2019) and other studies which find either a slight decline (Klink *et al.* 2020) or no decline (Crossley *et al.* 2020) is probably partially due to a baseline problem. Indeed while Hallman *et al.* (2017) and Powney *et al.* (2019) used a baseline older than 1990, the meta-analyses from Crossley *et al.* (2020) and from Klink *et al.* (2020) used a majority of datasets starting after 1990, the median of the starting year being 1992 over the two studies (**Figure III-2c**). The fact that a majority of datasets use a recent baseline likely explains partially the differences between the results of these meta-analyses and studies showing strong decline.

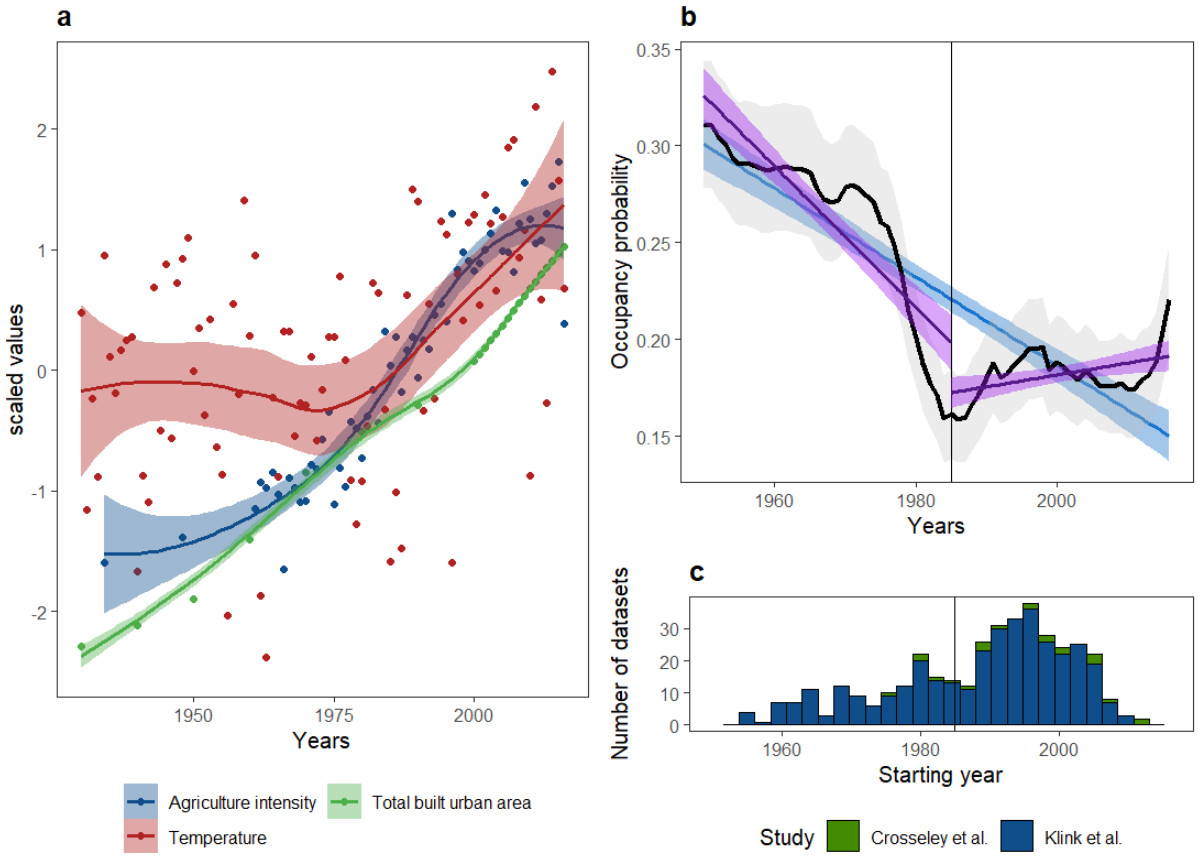

Figure III-2: ***Temporal dynamics of global change drivers and of occupancy of wild bees and temporal distribution of recently used datasets on insects.*** *(a) scaled (centered by mean and scaled by standard deviation) values of the global change drivers (points) and their smoothed trends (lines) in Belgium. (b) Predicted variation of occupancy probability across years averaged over 205 species ofwild bees in Belgium (black line), from Appendix II. Blue line shows the overall temporal linear trend while purple lines show linear trends on 1950-1985 and on 1985-2016. Ribbons show the CI95% confidence interval. (c) Distribution of starting years of datasets used in two recent meta-analysis focusing on insect biomass and abundances (Crossley et al. 2020; Klink et al. 2020), the vertical line representing the year 1985. 5 datasets older than 1950 were not represented here to keep constant x-axis scales.*

Short-term temporal dynamics, over the season

Since we assessed species responses of a wide diversity of species, our results allowed us to generalize results about known average responses to global change over time, but also to highlight a high variance among species responses associated to this mean. Regarding phenological and geographical range shifts, this heterogeneity is key to understand how species responses to global change affect communities. If there is variation in the way species respond to a perturbation, we expect modifications at the community level, which is not the case if there is no variation in those species responses.

Changes in the seasonal structure of pollinator assemblages

Since species phenological shifts are heterogeneous, combining them at the species assemblage level modifies the seasonal structure of those species assemblages. Such modifications have already been documented in plant communities with no clear pattern emerging, phenological shifts leading either to an increase of overlap in flowering periods among species (Theobald *et al.* 2017), to no clear average pattern (CaraDonna *et al.* 2014) or to a decrease of the overlap (Diez *et al.* 2012). Because changes in overlap will change inter-specific interactions, such as mutualistic interactions or competition in pollination networks, they are expected to affect ecological functions (Theobald *et al.* 2017).

Here we have been able to reveal that shifts in pollinator flight periods modified the seasonal structure of European pollinator assemblages, which likely altered their functional redundancy and complementarity (**Appendix I**). Then, focusing on wild bees in Belgium (**Appendix II**), we further showed that the synergic effects of bee decline and flight period shifts resulted in a shorter pollination season, with lower species richness and abundance, compared to historical pollinator assemblages, implying a sharp decline in pollination services and functions. Those two studies show pernicious effects of phenological shifts due to global change, visible only if we look at them at the scale of species assemblages. Our results along with other studies (Diez *et al.* 2012; CaraDonna *et al.* 2014; Theobald *et al.* 2017; Carter *et al.* 2018) participate to bridge species responses to global changes and ecological functions by showing that changes in the seasonal structure might have led to decrease the functional redundancy and complementary of European pollinator assemblages.

In the **Appendix II** we have highlighted synergistic effects between changes in occupancy and phenological shifts on the seasonal structure of a wild bee assemblage, due to a correlation between those changes. Correlation among species responses to global change, leading to synergistic effects among them, is probably common, because those responses are strongly linked through a common species evolutionary trajectory. For example, it has been shown that limited dispersal abilities, preventing geographic range shifts, can accelerates ecological niche shift (Aguilée *et al.* 2016), thus creating a negative correlation between geographical range shifts and physiological evolution. If such correlation among species responses is common, synergistic effects among those responses could be not rare. This highlights the fact that focusing on one kind of species responses to global change, as most of the studies do, can lead to misestimate global change effects on biodiversity. However, studying multiple species

responses together by accounting for these putative correlations remains a challenging task, on which evolutionary ecology should work to better understand our changing world.

The seasonal structure promotes diverse communities

Our theoretical model of pollination networks also allowed us to assess what are the consequences of the seasonal structure on network properties, especially diversity at equilibrium, also called network persistence (Saavedra *et al.* 2011). Our results (**Appendix V**) showed that phenologies structure ecological networks in a way that favors a less negative balance between facilitation and competition among species from the same guild, thus maintaining higher diversity than when the seasonality of interactions is neglected. Very few studies included phenologies in theoretical models so far (Kallimanis *et al.* 2009; Encinas-Viso *et al.* 2012; Revilla *et al.* 2015; Ramos–Jiliberto *et al.* 2018), and to my knowledge only two of them tried to investigate mechanistically the consequences of the seasonality in interactions at the network level (Encinas-Viso *et al.* 2012; Ramos–Jiliberto *et al.* 2018). As the seasonal structure is important to maintain diversity in mutualistic communities, and because it is a non-random structure evolved for many time (Jones *et al.* 2012; Maeng *et al.* 2012), any change in the seasonal structure, such as the ones documented above, is likely to lead to a cascades of extinctions.

On the importance of competition in mutualistic networks

The previous paragraphs have highlighted the importance of the seasonal structure to maintain diversity in mutualistic networks, but also the importance of competition in ecological communities. To me, this is a main result of this PhD, as the role of competition in mutualistic networks has been poorly studied (Levine *et al.* 2017). Indeed, competition can result from a biological indirect interaction associated with sharing the same resources but itthat is often studied through models of small interaction motifs focusing on pairwise mechanisms of species coexistence (Levine *et al.* 2017) or implemented without accounting for interaction structure, assuming that all species of the network compete with each other with identical intensities (Bastolla *et al.* 2009). In this part I will discuss a bit on how I believe that my results highlight the importance of the competition in shaping mutualistic networks in a changing world.

Competition and the seasonal structure

A balance between competition and facilitation

In the **Appendix V** we considered mutualistic interactions among plants and pollinators, but also competition within guilds, both structured by phenological and morphological traits. Our original approach merged with the nice theoretical work from Nakjima & Higashi (1995), allowed us to show that the seasonal structure of mutualistic networks favors facilitation over competition, when accounting for indirect effects occurring through long paths. Elegant mathematical demonstrations have shown that indirect effects between species, the consequence of indirect interactions, occur through long-paths, which should play an important role in any ecological networks (Higashi & Nakajima 1995; Nakajima & Higashi 1995), for example through *the alteration in sign of interactions between a pair of species due to the change in dominance among the effects carried by parallel paths connecting the species* (Higashi & Nakajima 1995). However, almost no study has considered these effects through long paths in mutualistic networks, except recent pioneering works showing that they affect evolutionary dynamics of species (Guimarães *et al.* 2017) and network robustness to perturbation (Pires *et al.* 2020). Our results highlight once again the importance of these indirect effects in a network context, and provide a mechanistic understanding of the importance of seasonal structure of communities to maintain diversity, thus completing and generalizing pioneering results on pairwise species models (Rudolf 2019). Our results also suggest that changes in the seasonal structure because of phenological shifts, should affect communities through changes in direct-interactions, but also in indirect interactions, such as competition.

Robustness of mutualistic networks to phenological shifts depends on competition

Our simulations of phenological shifts in a network context had shown that network robustness to phenological shifts strongly depends on the value of the parameter setting the intra-guild competition strength in the network. When competition is null, networks are robust and resistant, while when competition is strong networks are not resistant and are moderately robust, echoing results from pairwise species models (Rudolf 2019) and empirical ones (Alexander & Levine 2019; Carter & Rudolf 2019). Once the general parameter setting the intra-guild competition strength in the network is fixed at a given value, our theoretical model allowed us to decouple the part of changes in abundance due to changes in competition

coefficient among species and the part due to the loss/gain of mutualistic interaction when phenologies are shifting. We showed that the loss of mutualistic interaction is the main driver of abundance changes but that the effect of changes in competition becomes non-negligible when phenological shifts are heterogeneous.

Our results also provide evidences that plant-pollinator interaction networks are under multiple pressures, and that some of this pressure will intensify, such as climate warming or urbanization, at least for a few decades. It has been shown that mutualistic communities can suddenly collapse because of reaching a tipping point (Lever *et al.* 2014). *Tipping points are crossed when small changes in external conditions trigger the sudden collapse of a system to an undesirable state that is usually difficult to reverse* (Dakos & Bascompte 2014). However, the study of those community collapse are relatively out of touch with biological mechanism, because they model an unstructured competition (Dakos & Bascompte 2014; Lever *et al.* 2020) while competition is key to understand feedback loops determining tipping points (Lever *et al.* 2020). I think that including the seasonality of plant-pollinator interaction in those models can allow to anchor theoretical models in biological mechanisms and can teach us how communities could react to increasing pressures from global change.

A trace of competition in species response to global change?

Does competition mediate the surprising climatic bonus of Mediterranean plants?

In addition to moving in time, species shift their range, also modifying competition pressures over space (Alexander *et al.* 2015). By assessing the relationship between the decoupling between plants geographic range and historical climatic conditions and species occupancy trends, we showed that European plants lagging behind climate change pay a climatic debt in the North, but are favored in the South. The first point provide one of the first empirical evidences, to my knowledge, that plants are already paying their climatic debt. The second point is surprising and may suggest a role of inter-specific interactions in mediating this climatic bonus for southern plants lagging behind climate change over space. Indeed, plants with limited or no northward shift (i.e. plants with an increasing temperature SCI) may benefit from competitive release associated with the range shift of more mobile species, without being in competition with novel competitors from southern regions, because of the numerous geographic barriers limiting plant colonization in the Mediterranean region (Normand et al. 2011). This results also suggest that if we already know that global change can lead to species extinction

through increase in competition pressures, it can also led to species thriving because of a decrease in competition pressures, at least temporarily.

Is the competition involved in phenological shifts?

Moreover, species can also evolve to buffer changes in competition pressures. The buffering of demographic costs due to an environmental change by an evolutionary response is often called evolutionary rescue (Carlson *et al.* 2014). Such evolutionary rescue has been mainly theorized in a monospecific framework, but it had recently been brought extended to a network context (Loeuille 2019). Again, considering evolutionary rescue puts the spotlight back on the competitive exclusion principle, theorized by Darwin (Darwin 1859) and then by Gause and Volterra (Volterra 1928; Gause 1934). Indeed, as shown above, the competition mediates species persistence in a network context, thus probably acting as an evolutionary driver, at least partially. Our results suggest that the signal of evolution detected in the phenological shifts is affecting the seasonal structure of pollinator assemblages in a non-random way, mostly by decreasing the phenological overlap among species (**Appendix IV**). This could suggest an evolution of the pollinator mean flight date in response to changes in the competition pressure, due to plastic phenological shifts, or to a floral resource decline (Biesmeijer *et al.* 2006; Scheper *et al.* 2014). Such result echoes previous theoretical (Loeuille 2019) and empirical (Alexander & Levine 2019; Carter & Rudolf 2019) findings. However, new methodological approaches need to be developed to fully integrate phenological shifts in a community framework. Such approaches could be for example the use of Joint Distribution Models used to model species distribution (Pollock *et al.* 2014) or species trait evolution (Bastide *et al.* 2018) taking into account inter-specific relationships. Such methods, coupled with the fact that monitoring scheme developed recently will begin to have accumulated mid-term time-series (~20 years), will open the door to inferring evolution on a wide set of species, over large spatial scales. However, such work would also need to correct putative bias from opportunistic datasets, a tricky task, even with sophisticated methods.

Opportunistic data *vs* protocoled data

An important part of the results of this PhD is based on opportunistic data. Although it is easy to find publications to argue that opportunistic data can provide accurate estimate of phenological shifts (Robbirt *et al.* 2011; Bishop *et al.* 2013b; Hassall *et al.* 2017) or occupancy

trends (Isaac *et al.* 2014; Outhwaite *et al.* 2019), it is worth to remain critical about the fact that an important part of our scientific knowledge on some topics is from non-protocoled data. First, it shows that we lack time-series of protocoled data for many taxa and many areas, stressing the need to develop new monitoring schemes on a wide diversity of taxonomical/functional groups and to maintain existing schemes. Second, since those data are biased in many ways, because of temporal changes in the way that they are collected, it can be misleading. Indeed, in those datasets, historical records are mainly from experts and specialists, who often collected preferentially rare species, while more recent data are from open citizen sciences, which mainly focus on common species. Moreover, because of the opening of publicly available database to stock nature observations, the number of records is increasing exponentially over time, leading to dramatic shifts in the effective sampling pressure. Those changes are likely to bias temporal trends in occupancy, for example, if they are not accounted for, thus challenging our ability to extract information from this kind of dataset.

Accounting for temporal changes in species detection probability

In this PhD, to estimate wild bee occupancy trends we used a sophisticated method that have been developed to take into account a part of putative bias (Isaac *et al.* 2014; Outhwaite *et al.* 2018). First, we inferred pseudo-absence from presence data, by inferring the pseudo-absence of a focal bee species at a given location and date when at least one other bee species was detected at the same location and date but not the focal species. Such inference of pseud-absences, by transforming the dataset from presence data only to a presence-absence dataset, allows to correct by the sampling pressure. Then we modeled presence-absence data by using an occupancy model accounting for detection probability and for temporal changes in this detection probability. Such "detection probability" also encompasses a bit more than just detection as it represents the detection probability plus the registration probability in the database. Thus, our method takes into account that museum collectors in the past were more likely to target rare species than now. For example, we can see for the common species *Bombus lapidarius* that its detection probability has increased over 1960-2016, as expected for such common species which was not collected much by collectors in 1960-1980 (**Figure III-3a**). Moreover, assessing this trend for all species, we show here that the temporal trend in detection probability is linked to the total number of data recorded for the species (**Figure III-3b**). Species characterized by fewer records tend to have a detection probability that decreases over time while species with many records tend to have an increasing detection probability. This

result suggests, as we expected, that rare species were more detected in the past, in contrast to common species. These results suggest that the method used in our study is able to account properly for changes in detection probability when estimating occupancy trends.

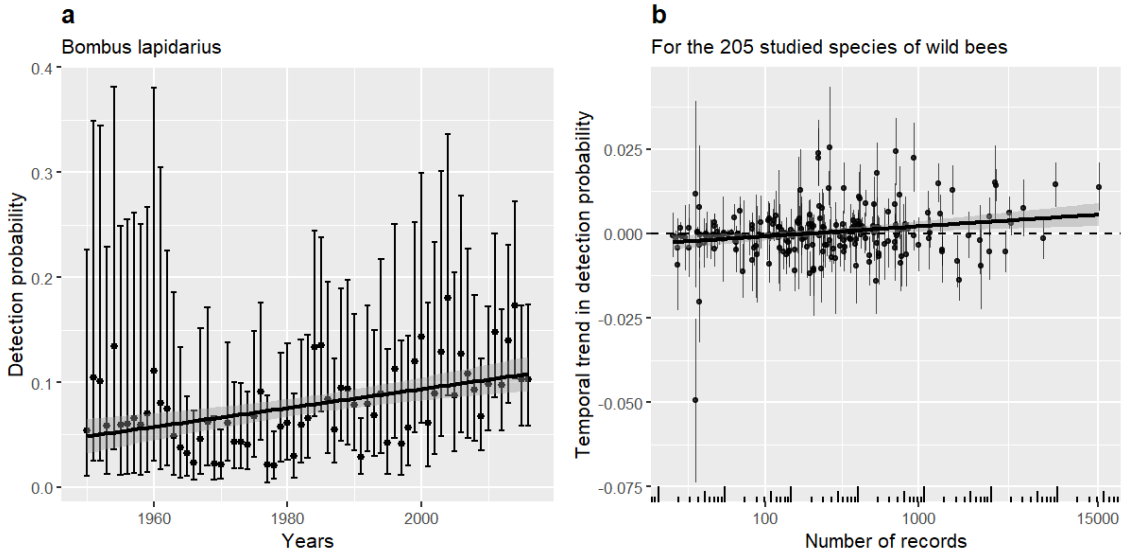

Figure III-3: ***Temporal trend in detection probability of species.*** *(a) Detection probability in function of the years for Bombus lapidarius or (b) in function of the logarithm of the number of records for all species. In (b) rare species are on the left of the x axis (few data) while common species are on the right of the x axis (lot of records). Lines are simple linear trends. Error bars and ribbons are 95% confidence interval.*

A test against protocoled data from citizen sciences

However, this method was tested only against simulated datasets (Isaac *et al.* 2014) and it has never been tested against results from protocoled datasets. In what follows, we compared occupancy trends estimated from two datasets. The first one is a protocoled dataset monitoring French plant occupancy, Vigie-Flore (Martin *et al.* 2019), and the second is an opportunistic dataset containing distribution records of French plants, from the *Conservatoire Botanique du Bassin Parisien* (CBNP, http://cbnbp.mnhn.fr/cbnbp/). To estimate occupancy trends from Vigie-Flore, we used the same method that Martin *et al.* (2019) but applied on the data collected between 2009 and 2019 and only in *Île-de-France* region. To estimate occupancy trends from the CBNP dataset, we used the method from Isaac *et al.* (2014), corresponding to the method described above, applied on the data collected between 2009 and 2018 and from *Île-de-France* region too. Although they were calculated for the same species in the same region, on comparable time periods, we do not find any correlation between these two sets of occupancy trends (**Figure III-4**). We are currently unable to explain the differences in estimated occupancy

trends between both datasets, and we do not know where the truth is[8]. This result shows that opportunistic datasets and protocoled datasets can give strongly divergent results, stressing the need to develop statistical tools to compare different datasets and to analyze as much as possible different datasets to evaluate how results depends on the data source.

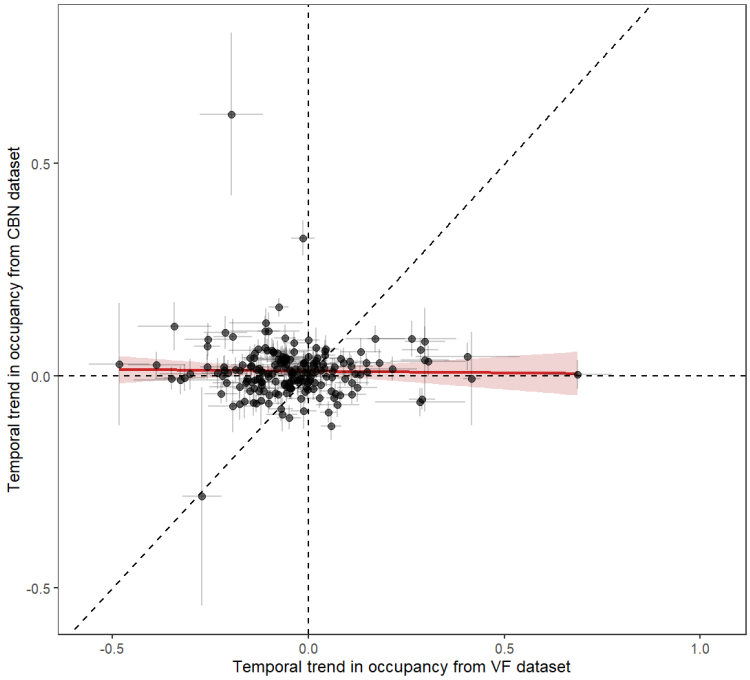

Figure III-4: ***Comparison between occupancy trends of french plants from a protocoled dataset and from an opportunistic dataset.*** *Red line is a simple linear trend and error bars are 95% confidence interval.*

[8] "*Theory is when you know everything but nothing works. Practice is when everything works, but nobody knows why. We have put together theory and practice: nothing is working, and nobody knows why.*" Albert Einstein

IV. Conclusion

In this PhD we analyzed temporal dynamics of biodiversity to assess how global change has affected species and communities whilst avoiding the space-for-time substitution pitfalls. All together the results presented showed that species are responding over time and over space to global change, and that these responses are strongly constrained by geographical and seasonal niches, as well as by evolutionary history. Those constraints create heterogeneity in the way species respond to global change, thereby affecting the seasonal structure of communities and/or their composition over space. Such changes at the community level are likely to affect community stability and functioning, by disrupting direct interactions and by affecting indirect interactions, such as competition and facilitation. Finally, we showed that when accounting for the seasonality of interactions among species, those indirect interaction play a major role in community and species persistence, while they are widely overlooked in ecological network studies. Together, these projects constitute a modular interconnected body of studies (C = 0.25, NODF = 3.87, Modularity = 0.36), tackling different facets of the relationship between global change and biodiversity (**Figure IV-1**).

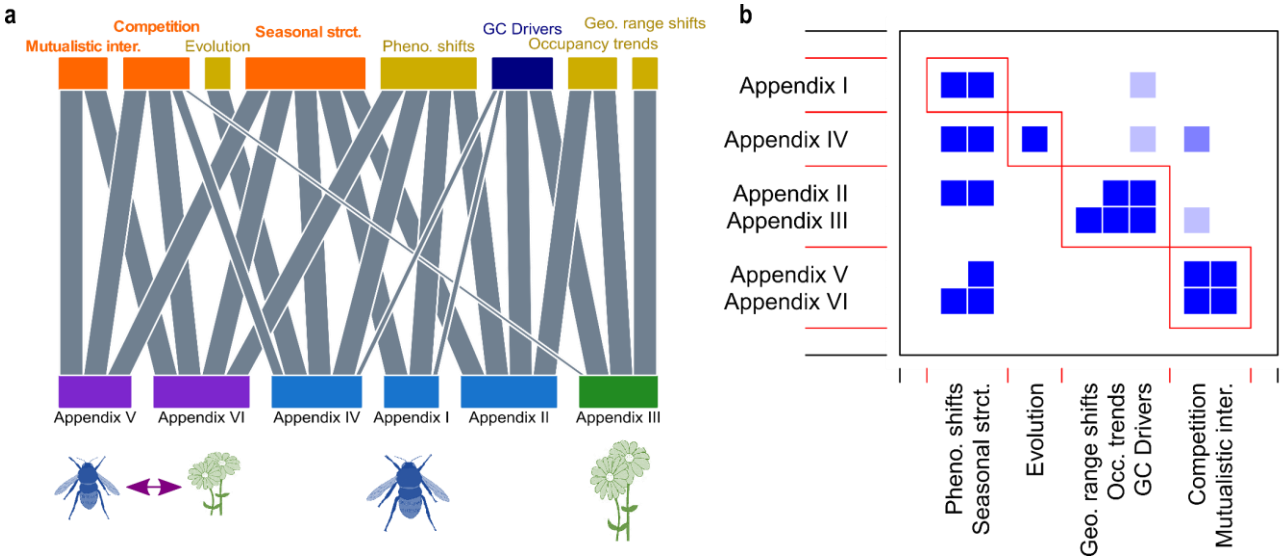

***Figure IV-1:* Connections among all my PhD projects and different facets of the biodiversity-global change relationship**. *(a) higher level represent main facets tackled in my PhD, from species responses to global change (yellow), community level changes (orange) and global change drivers (dar blue, GC drivers). Lower level represents the different projects included in my PhD, from theoretical studies of polliantion networks (purple), or empirical studies focused pollinator (blue) and plant (green) responses. (b) Matrix representation of this networks and modules found by a Newman's mod-ularity measure. Geo. Range shifts= Geographic range fhist; Pheno. shifts = Phenologicla shifts; Mutualistic inter. = Mutualistic interactions; Seasonal strct = Seasonal structure.*

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VI. List of figures

VII. List of tables

VIII. Annexes

Appendix I

Duchenne F., Thébault E., Michez D., Elias M., Persson M., Rousseau-Piot J. S., Pollet M., Vanormelingen P. & Fontaine C. Phenological shifts alter the seasonal structure of pollinator assemblages in Europe. *Nat. Ecol. Evol.* **4**, 115–121 (2020). https://doi.org/10.1038/s41559-019-1062-4

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Phenological shifts alter the seasonal structure of pollinator assemblages in Europe

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Pollinators play an important role in terrestrial ecosystems by providing key ecosystem functions and services to wild plants and crops, respectively. The sustainable provision of such ecosystem functions and services requires diverse pollinator communities over the seasons. Despite evidence that climate warming shifts pollinator phenology, a general assessment of these shifts and their consequences on pollinator assemblages is still lacking. By analysing phenological shifts of over 2,000 species, we show that, on average, the mean flight date of European pollinators shifted to be 6 d earlier over the last 60 yr, while their flight period length decreased by 2 d. Our analysis further reveals that these shifts have probably altered the seasonal distribution of pollination function and services by decreasing the overlap among pollinators' phenologies within European assemblages, except in the most northeastern part of Europe. Such changes are expected to decrease the functional redundancy and complementarity of pollinator assemblages and, therefore, might alter the performance of pollination function and services and their robustness to ongoing pollinator extinctions.

Numerous studies on plants, birds, amphibians and insects reveal that on average various phenological events—such as flowering or initiation of flight season—now take place earlier in the season than in the past decades because of climate warming[1]. Despite this general trend, a substantial inter-specific variation is observed in these responses, spatially[2] (for example, across latitudes) and temporally[2,3] (for example, spring versus summer species). This heterogeneity in species responses together with the fact that most studies focus on taxonomic rather than functional groups[1] challenges our ability to assess the consequences of phenological shifts for the functioning of communities and ecosystems across large spatial scales.

By modifying the set of species co-occurring in time, heterogeneity in phenological responses can induce mismatch among interacting species[4], thereby affecting community structure and related functions. One key issue to our understanding of the impact of climate warming on ecological functions is thus to assess how phenological shifts combine themselves among the species assemblage involved in a given function. This requires us to quantify the phenological responses of a large proportion of the species, not only in terms of mean flight date (MFD) shifts but also of changes in phenology length, a currently overlooked aspect of species responses[5]. The few studies that started to tackle this issue revealed important changes in patterns of species temporal overlap in several local communities of plants and amphibians, as a result of non-uniform phenological shifts[4,6,7]. However, these studies remain restricted to a small set of functional or taxonomical groups and to a small set of local communities.

Pollination is a key ecosystem function[8,9] mainly performed by four insect orders in Europe: Hymenoptera, Diptera, Lepidoptera and Coleoptera[10]. These flower visitors present a continuum of pollination efficiency, but the diversity within pollinator assemblage has been proved to increase pollination performance[11]. Current theoretical knowledge indicates that the level of heterogeneity in phenological responses to climate warming among pollinators can strongly affect pollination networks[12]. However, the quantification of the phenological responses of pollinators to climate warming is still limited, with studies focused on butterflies[13,14] and, to a lesser extent, on bees[3] and hoverflies[15]. A better understanding of the consequences of climate change on pollination thus requires a much more complete assessment of changes in pollinator phenology, including more species and changes in both timing and duration of the seasonal activities.

We took advantage of recent developments of large biodiversity databases and museum collections and we compiled a database of over 19 million records of flower visitor occurrences (Supplementary Table 1), spanning the period 1960–2016. This database includes 2,023 European species from the 4 main insect orders of pollinators: Hymenoptera, Diptera, Lepidoptera and Coleoptera (Extended Data Fig. 1). Numerous species exhibit distinct modes in their phenology, either because they are multivoltine (that is, multiple generations per year) or because the phenology differs between sexes or social casts. Since different modes from a species can shift in a different direction, we studied each mode separately, leading to 2,248 phenology modes (see Methods). For each phenology mode, we estimated changes in MFD and flight period length (FPL) over the years by modelling the mean and variance of collection dates (see Methods). Similarly to previous studies working with historical records[3], due to the lack of long-term standardized monitoring for many flower visitor taxa and at large spatial scales, our analysis relies on opportunistic data. However, such datasets have been shown to give estimates of phenological shifts quantitatively consistent with those based on standardized monitoring data[15,16].

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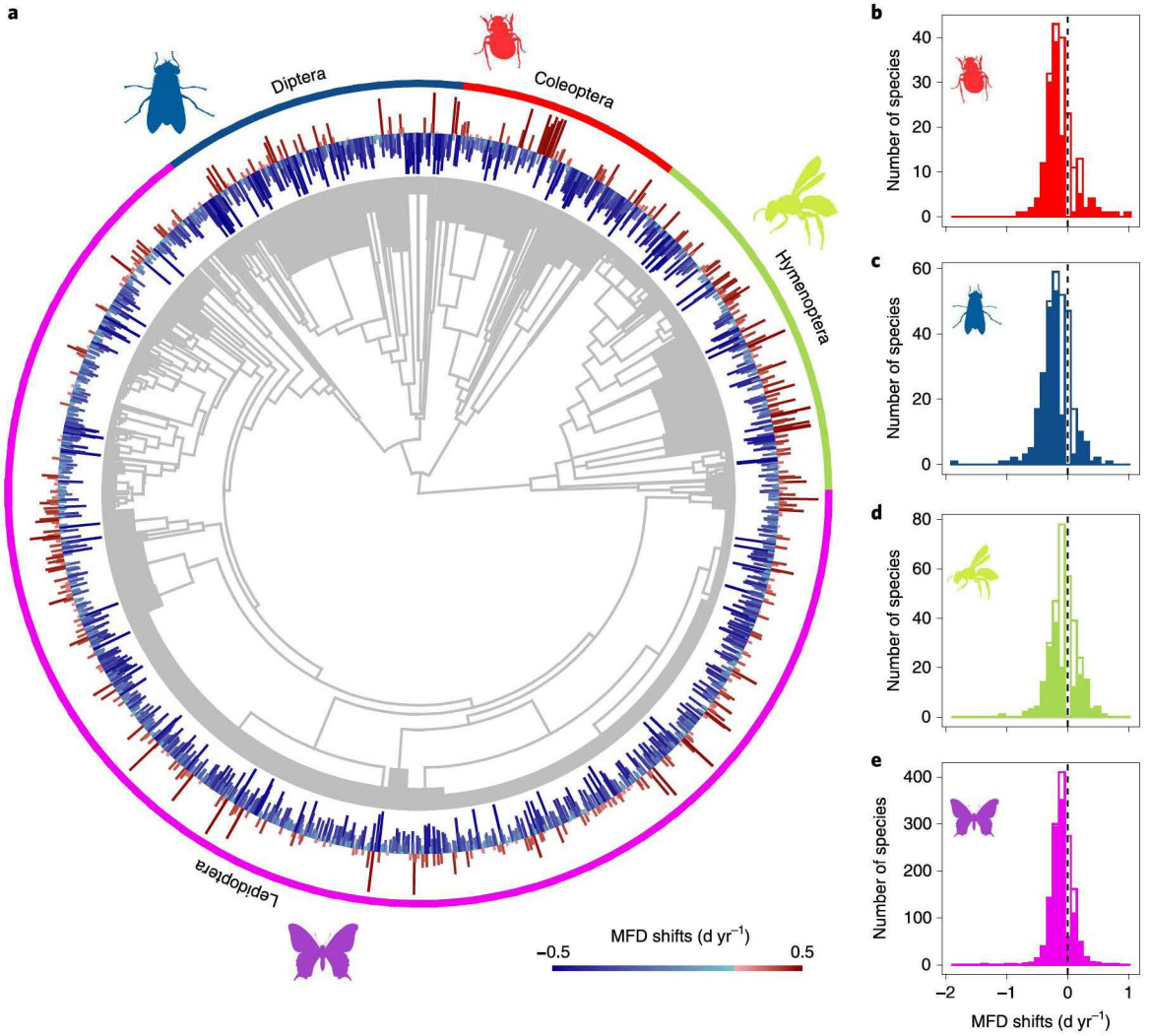

Fig. 1 | MFD shifts of European flower visitors between 1960 and 2016. a, Phylogeny of the studied species and MFD shifts ($n = 2{,}248$). The bars around the phylogeny tips are proportional to the MFD shifts and coloured in blue and red for phenological advancement and delay, respectively. Values below −0.5 and above 0.5 d yr^{-1} are truncated to preserve readability. **b**–**d**, Histograms show MFD shifts for all studied species of Coleoptera (**b**, red, $n = 194$), Diptera (**c**, blue, $n = 305$), Hymenoptera (**d**, light green, $n = 322$) and Lepidoptera (**e**, magenta, $n = 1{,}427$). Filled bars represent the number of species with values significantly distinct from zero; open bars correspond to the number of species with a value non-significantly distinct from zero (dashed line). The MFD shifts shown here are predicted for the averaged latitude, longitude and altitude of each species' records.

Results

We find that the MFD changes on average at a rate of -0.104 ± 0.004 d yr^{-1} (mean ± s.e.m.) implying that European pollinators are flying on average 5.8 d earlier in 2016 than in 1960, a value consistent with previous estimations on bees[3] and butterflies[13]. Climate warming appears as a likely cause as MFD shift mainly occurred after 1980, following the temperature increase (Supplementary Method 1 and Extended Data Fig. 2). Considering FPL, we find that on average the standard deviation of collecting dates decreases slightly with time, at a rate of -0.016 ± 0.003 d yr^{-1} (mean ± s.e.m.), which corresponds to a decrease of 1.8 d of the FPL over the last 56 yr. This reduced FPL might be due to a reduced genetic variability on phenology caused by a directional selection on phenology advancement. Indeed, we know that a directional selection on a phenotypic trait can reduce the variance of this trait[17], and the significant positive Pearson correlation between the changes over time of MFD and FPL ($r = 0.09$, $t_{df=2,246} = 3.89$, $P = 1 \times 10^{-4}$) can suggest such a mechanism. However, whether these changes are adaptive or not, and the mechanisms underlying these responses (adaptation versus phenotypic plasticity), remain unknown.

Despite these overall trends, we observe a substantial heterogeneity among species in the response of MFD and FPL (Fig. 1 and Extended Data Fig. 3). Of the phenologies studied, 13% exhibit a significantly delayed MFD whereas 30% do not exhibit any significant shift (Supplementary Table 2). Such heterogeneity is even more striking for FPL changes, where 27% of the phenologies studied are significantly lengthened and 43% are unchanged (Supplementary Table 2). If an increase of winter temperature is known to advance species phenology by reducing the development time[18], some species also react in an opposite way[18,19], which might explain observed variations in MFD shifts. Turning to the heterogeneity in FPL responses, a temperature increase can either reduce or increase FPL (for example, by reducing insect lifespan[20] or by increasing the number of generations within years[14]).

We further show that this heterogeneity in phenological responses is related to the evolutionary history of species as shown by the strong phylogenetic signal in MFD shifts (Pagel's $\lambda = 0.75$, $P < 0.001$) and in FPL changes (Pagel's $\lambda = 0.82$, $P < 0.001$). This phylogenetic signal is related to strong differences among orders in these phenological shifts, Diptera and Coleoptera advancing their

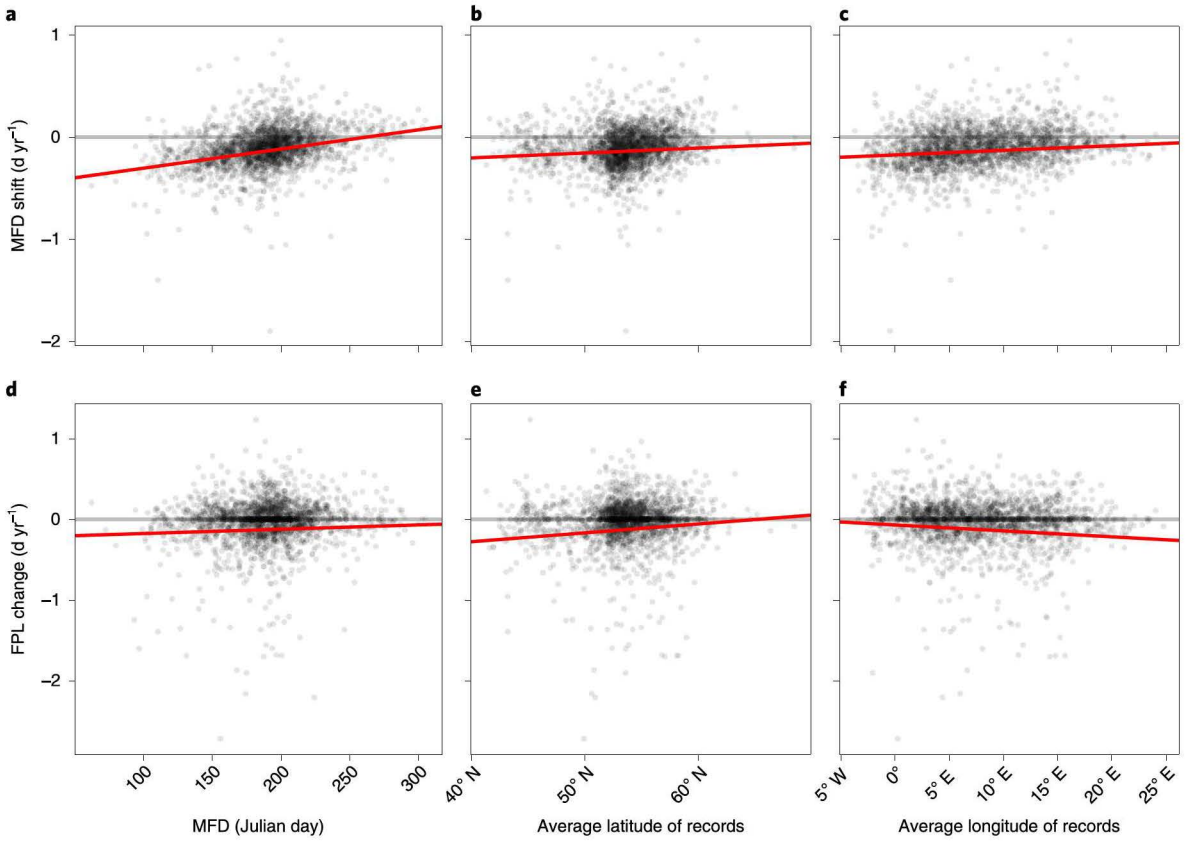

Fig. 2 | Spatial and seasonal heterogeneity in phenological shifts among species. a–f, MFD shifts (**a–c**) and changes in FPL (**d–f**) against species MFD (**a**,**d**) and averaged latitude (**b**,**e**) and longitude (**c**,**f**) of species records. Horizontal grey lines show the 0 value; red lines are phylogenetic generalized least-squares predictions. Estimates and standard errors are shown in Supplementary Table 4.

MFD more than Lepidoptera and Hymenoptera while Coleoptera decrease their FPL more than the other orders (Supplementary Table 3). However, the phylogenetic signal remains significant within orders for MFD shifts (Supplementary Table 3). This phylogenetic signal indicates that species traits underlying phenological responses are conserved across the phylogeny.

MFD and FPL responses also demonstrate spatial and seasonal heterogeneity among species. Species with southern and western distribution areas show a stronger MFD advancement than species with northern and eastern distribution areas (Fig. 2b,c and Supplementary Table 4), matching previous results on European plants[2]. We also find that species with northern and western distribution areas experience a smaller decrease in FPL than species with southern and eastern distribution areas (Fig. 2e,f and Supplementary Table 4). In addition, we find a seasonal pattern where spring species experience a significantly greater advancement than summer/autumn species (Fig. 2a), consistently with previous results on American bees[3] and European plants[2]. Regarding FPL, we find that earlier species shorten their flight period more than later species (Fig. 2a–d and Supplementary Table 4). Such differences could be explained by the fact that summer/autumn and northern species might rely more on photoperiod, a determining factor of insect phenology[21], than spring and southern species. Such patterns have been shown for plants[22,23], but studies on this point for insects are missing.

We further show that the MFD shifts vary within species in a way that echoes the patterns found at the inter-specific level. Indeed, we detect a significant positive interaction between the latitude and year effects for 29% of species, indicating that southern populations experience a stronger shift of their MFD towards earlier dates than northern populations (Supplementary Table 2). By contrast, no longitudinal pattern was found. The seasonal pattern of stronger advancement earlier in the season is also found at the intra-specific level. Among the 190 species with multimodal phenology and sufficient data to study them, 59% have their first mode advancing significantly faster than their second mode while the opposite pattern occurs only in 10.5% of the species (Extended Data Fig. 4).

To assess the consequences of these phenological shifts for the seasonal structure of pollinator assemblages across space, we analysed changes in the phenological overlap of species co-occurring within locations of 5°×5° grid cells in Europe, between 1980 and 2016. We used the linear models for MFD and FPL to predict the phenologies of each species for each grid cell predicted for both years (Fig. 3a). Considering that all phenologies are unimodal, we modelled them by Gaussian density distribution, to calculate the pairwise phenological overlap among all pairs of pollinators present in a grid cell (see Methods). We averaged these measures among pollinators belonging either to the same or to different insect orders (see Methods).

First, we show that species co-occurrence in time increases towards the beginning of the season and then abruptly decreases in the second half of the season (Extended Data Fig. 5), consistently with the average advancement of pollinator MFD. This indicates that the advance of MFDs has probably shifted the pollination function and services to earlier in the season. Second, assuming no changes in abundance/distribution of species, we show that both within- and among-orders average overlaps in phenology have decreased within the last 36 yr in most parts of Europe, except in the extreme northern

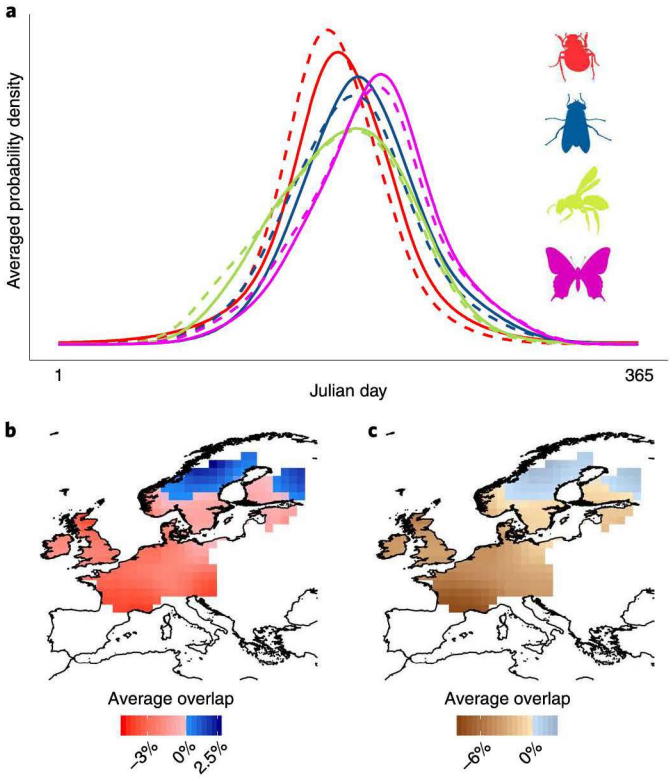

Fig. 3 | Changes in within- and among-orders average overlaps in phenology between 1980 and 2016 across Europe. a, Average phenology over all species in 1980 (solid lines) and in 2016 (dashed lines) for one grid cell (centroid = 55,0) by orders: Coleoptera (red), Diptera (blue), Hymenoptera (light green) and Lepidoptera (magenta). The average phenology is calculated by averaging all probability density functions (Gaussians representing phenologies) over all species of each order, assuming identical species abundances. **b**,**c**, Observed changes in the average overlap among phenologies between 1980 and 2016, within orders (**b**) and among orders (**c**). Uncoloured cells are under-prospected. The number of species by order across Europe is shown in Extended Data Fig. 6.

part (Fig. 3b,c). The observed increase of the overlap among phenologies in northern Europe is probably due to the fact that there, in contrast to other regions, the average MFD shift is almost null whereas the FPL slightly increases (Fig. 2). Sufficient data on long-term dynamics of plant–pollinator networks are currently missing to fully assess the consequences of such changes in the seasonal structure of pollinator assemblages on pollination function. However, the within-order and among-order overlaps should be related to temporal redundancy and complementarity within pollinator assemblages, respectively. Indeed, the pervasive phylogenetic signal within pollination networks indicates that related pollinators tend to visit the same plants[24,25]. This implies that species with overlapping phenologies and belonging to the same insect order should visit the same set of co-flowering plant species and thus belong to the same pollinator functional group. By contrast, species with overlapping phenologies but from different insect orders are expected to provide a complementary pollination function, by visiting different sets of co-flowering plant species.

Therefore, the observed decrease in the overlap within insect orders, by lowering the temporal redundancy among pollinators, might decrease the robustness of plant–pollinator interaction networks to pollinator extinction[26]. A decrease in the overlap may also have beneficial effects for pollinators by decreasing competition for nectar and pollen resources, but such competition release might in turn restrict pollinator visits to the most profitable plant species following optimal foraging theory predictions[27]. Turning to the observed decrease in phenology overlap among pollinator orders, it suggests a decrease in temporal complementarity within pollinator assemblages, thereby weakening the pollination function delivered to plant communities[28]. This result echoes theoretical findings on pollination networks showing that the more phenologies are scattered over the season, the more community diversity decreases[29].

Discussion

Our results show that flower visitor responses to climate warming depend on their evolutionary history, geographical location and seasonal earliness. This high variation in species phenological responses is expected to drive heterogeneity in the consequences of climate warming on pollination function across Europe and across the season. For most parts of Europe, the observed modifications of the seasonal structure of pollinator assemblages are expected to have negative consequences on pollination, while in northeastern Europe they might have positive effects on pollination as they result in an increased phenology overlap, both within and among pollinator orders (Fig. 3). Moreover, in most parts of Europe, observed changes are expected to have a positive effect on pollination performance and robustness early in the season but a negative effect from the middle to the end of the pollination season (Extended Data Fig. 5). Thus, our results highlight the importance to assess responses at large spatial and temporal scales and to include many species, to capture the high spatial and seasonal heterogeneity in the consequences of climate change on pollinator assemblages and related function.

Climate warming is recognized as a major threat to biodiversity. Our results suggest that climate warming, by reducing pollinator co-occurrence in time within seasons, has had a negative effect on the delivery of pollination function as well as on its resistance to further perturbations, in most parts of Europe. Such findings raise the question of potential interactive effects between climate warming and other pressures related to global change such as agricultural intensification[30,31], which could amplify expected negative effects on pollination. In addition to its effect on species phenology, climate warming is expected to affect the spatial distribution[32] and the abundance[31] of flower visitors, and so are other drivers of global change. How such effects combine with those observed in this study remain unknown. This stresses the need to explore multiple responses of species to multiple drivers of global change to assess potential synergistic effects among species responses to global change drivers over large scales.

Methods

Constructing the database on flower visitor phenologies. *Assembling data on flower visitor occurrences in time and space.* European flower visitors mainly belong to four insect orders—Coleoptera, Diptera, Hymenoptera and Lepidoptera[10]. We first looked for occurrence data (that is, sighting at a given date and location) of species that belong to these insect orders and that are defined as floricolous in scientific or grey literature. We restricted our search to European species listed in Fauna Europaea[33]. The data are from 15 distinctive sources, summarized in Supplementary Table 1, with a high proportion from the Global Biodiversity Information Facility (GBIF). After the removal of duplicates (same species, date and locality), the database initially included about 30 million occurrences between 34° and 72° of latitude north and between −15° and 32° of longitude.

Modelling multimodal phenologies and removing larval records. Numerous species exhibit distinct modes in their phenology, either because they are multivoltine (that is, multiple generations per year) or because the phenology differs between sexes or social casts. Since different modes in the same species are temporally distant, they might not respond to the same environmental cues. As a consequence, each mode might potentially shift in a different direction and should thus be studied separately. Furthermore, larvae might be easier to spot than adults for Lepidoptera and some Coleoptera. Thus, a substantial proportion of records may actually be larvae, which are not floricolous and should be removed from the analysis. To split the occurrences of multimodal imago phenology into distinct modes as well as to identify larval occurrences, we developed the following method.

The first step of the method was to detect multimodality. Since phenologies vary spatially, multimodality can be the product of sampling in different localities.

To take this spatial variation into account, for each species separately, we fitted the following linear mixed-effects model accounting for spatial variables on the Julian day of the records:

$$Y_{ik} = \mu + \rho_1 \times \text{latitude}_k + \tau \times \text{longitude}_k + \theta \times \text{altitude}_k + \varphi_i + E_{ik} \quad (1)$$

where Y_{ik} is the Julian day of the observation k of the year i, μ is the grand mean (intercept), ρ_1 and τ_1 are latitude and longitude effects, respectively, and θ is an altitude effect. φ_i is a random year effect (factor) and E_{ik} is the error term (independent and identically distributed, following $N(0,\sigma^2)$). The residuals of this model thus represent the collection dates once spatial and altitudinal variations have been removed. To detect multimodality in the distribution of these residuals, we smoothed the distribution with the R function density, using the value 1.3 for the adjust parameter and counted the number of local maxima (nbmax) that reaches 7% of the highest mode. We used this cutoff to remove small peaks on the edges of the phenology and we defined the value of the threshold after a visual inspection of phenologies. Several modes were initially detected for 494 species. For each of these species, we checked in scientific and grey literature whether a multimodal phenology was expected. In 208 cases, there was no strong biological support of existing multimodal phenology and we thus considered these species had one single mode. After this step, 288 remaining species showed a multimodal phenology (nbmax > 1). We applied the second step only for these species.

The second step of the method was to attribute each record to a specific mode. To do so, we used clustering Gaussian mixture models implemented in the mclust R package[34], considering a number of Gaussians from one to nbmax. This clustering model allows us to initialize the attribution of each record to a given mode. Using the classification given by these clustering models, we run linear mixed-effects models, similar to the one described in equation (1) but with the addition of a mode effect (β_j):

$$Y_{ijk} = \mu + \rho_1 \times \text{latitude}_k + \tau \times \text{longitude}_k + \theta \times \text{altitude}_k + \beta_j + \varphi_i + E_{ijk} \quad (2)$$

We kept the number of modes that minimize the Bayesian information criterion of this linear mixed-effects model. We then manually changed the mode of poorly predicted points. If the change improved the likelihood of this mixed-effects model, we retained it and continued this process iteratively. We stopped the process when changing the mode of poorly predicted points did not further improve the likelihood of the model. The R script of the full method is available at https://github.com/f-duchenne/Flower-visitors-phenology. Although the mode effect (β_j) is independent from the spatial variables and altitude in equation (2), our method still allows us to take into account spatial and altitudinal variation in the number of modes (Extended Data Fig. 7). We confronted the relevance of detected modes regarding what we know on the biology of species. We found that our method distributes records among modes in a highly consistent way. Some examples can be seen in Extended Data Fig. 7. We identified 19 species for which we had a mode corresponding to larval phenology, and we removed the corresponding records. Overall, this analysis led to 2,473 unimodal phenologies from 2,179 species.

Database after selection process. Following the separation of distinct phenological modes for each species and the removal of larval records, we selected phenologies (or phenological modes) with at least 400 records during the period 1960–2016 and with at least 40 records from the period 1960–1980, to be able to study phenological shifts between early and more recent periods. We removed species ($n = 30$) with phenology peaking during winter by excluding species with a MFD before 60 or after 306 Julian days. Studying the phenology of such species raises methodological questions that we will not address here. We also removed records with imprecise localization (above 1 km²) except those for small countries (Luxembourg, Belgium, Switzerland, the Netherlands, Denmark, Lichtenstein, Monaco, Andorra and Kosovo). Thus, our dataset includes some records with imprecise localization (above 1 km²), but they represent less than 0.1% of the final dataset. This selection process led to 19,845,792 occurrence records with 2,248 phenologies for 2,023 species (Supplementary Table 1). The repartition of records among insect orders and throughout the study period is presented in Extended Data Fig. 1. Supplementary Table 1 indicates the amount of data coming from the various data sources.

Analyses of species phenological shifts over time. *Estimating species phenological shifts.* To estimate changes in both the MFD and the FPL, we modelled jointly the mean and the variance of collection dates using the dispmod R package[35], which performs two nested linear models, one for the mean and one for the variance. Due to computational limits, it was not possible to use one model including the whole dataset, modelling both MFD shifts and FPL changes, and modelling spatial effects properly for each species. Thus, we studied each species and phenology mode separately. For each phenology mode, the model for the mean collection date was:

$$\begin{aligned} Y_k = {} & \mu + \left(\pi + \alpha \times \text{latitude}_k + \delta \times \text{longitude}_k\right) \times \text{year}_k + \\ & \left(\rho_1 + \gamma_1 \times \text{longitude}_k\right) \times \text{latitude}_k + \left(\rho_2 + \gamma_2 \times \text{longitude}_k^2\right) \times \text{latitude}_k^2 \\ & + \left(\rho_3 + \gamma_3 \times \text{longitude}_k^3\right) \times \text{latitude}_k^3 + \tau_1 \times \text{longitude}_k + \tau_2 \times \text{longitude}_k^2 + \tau_3 \times \\ & \text{longitude}_k^3 + \theta \times \text{altitude}_k + E_k \end{aligned} \quad (3)$$

Y_k is the Julian day of the observation k, μ is the grand mean (intercept), and π is the time effect on the mean collection date as well as on its variation across latitude (α) and longitude (δ). ρ_1, ρ_2 and ρ_3 and τ_1, τ_2 and τ_3 are linear, quadratic and cubic effects for latitude and longitude, respectively, γ_1, γ_2 and γ_3 are spatial interaction terms, θ is an altitude effect and E_k is the error term (independent and identically distributed, following $N(0,\sigma^2)$).

The joint model for variance of collection date was:

$$\log\left(\sigma^2\right) = \mu_v + \rho_v \times \text{latitude}_k + \tau_v \times \text{longitude}_k + \theta_v \times \text{altitude}_k + \pi_v \times \text{year}_k \quad (4)$$

where σ^2 is the variance of the collection date, μ_v is a constant term, ρ_v, τ_v, θ_v and π_v are latitude, longitude, altitude and year effects, respectively. We performed model simplification based on the Akaike information criterion, first on the model for the mean collection date, removing only the polynomial effects of latitude and longitude (γ_1, γ_2, γ_3, ρ_2, ρ_3, τ_2 and τ_3) and interactions between the spatial variables and the time effect (α and δ), and second on the model for the variance in the collection date.

The MFD shifts presented in the paper are $\pi + \alpha \times \overline{\text{latitude}} + \delta \times \overline{\text{longitude}}$ from equation (3), where $\overline{\text{latitude}}$ and $\overline{\text{longitude}}$ are the averaged latitude and longitude of the species records, respectively. The FPL changes are the π_v from equation (4) for each species.

Phylogenetic analysis. To get a phylogeny of all the studied species, we combined several published phylogenies. We used the phylogeny from Rainford et al.[36] as the backbone to which we added some available and recent phylogenies to get a phylogeny at the genus level for Papilionoideae[37], Vespidae[38] and Apoidea[39]. For all other families, genera (as defined by the GBIF taxonomy) were inserted on a polytomy positioned midway between the family origin and the tip. Then species from each genus were placed on a polytomy positioned midway between the genus origin and the tip. This method does not allow a good estimation of the recent evolutionary history but because there is no phylogeny of insects at the species or genus level, it is the only way to include all species responses and account for intra-family heterogeneity. Moreover, because these polytomies were not too old relative to the entire phylogeny, it should not strongly affect our results. As they are not present in our phylogeny, three families of Diptera (Heleomyzidae, Limoniidae and Pediciidae) and two Lepidoptera species (*Sphrageidus similis*, Lymantriidae, and *Agria desoptilete*, Lycaenidae) were excluded from the phylogenetic analysis.

We estimated the phylogenetic signal in phenological shifts using Pagel's λ (ref. [40]) implemented in the phylosignal R package[41], because it is much more robust to polytomies than Blomberg's K (ref. [42]).

Links between phenological traits and phenological shifts. To test whether the seasonal precocity and the spatial distribution of species were linked to phenological shifts, we used the following phylogenetic generalized least-squares model implemented in the caper R package[43] controlling for Pagel's λ of the residuals at the maximum likelihood:

$$\text{PS}_z = \mu + (\alpha) \times \text{MFD}_z + (\beta) \times \text{latitude}_z + (\delta) \times \text{longitude}_z + E_z \quad (5)$$

where PS_z is the phenological shift (that is, MFD shift or FPL change) of the species z, μ is the grand mean (intercept), α is the effect of the MFD calculated with recent records (from 2000), β is the effect of the average latitude of records, ρ is the effect of the average longitude of records and E_k is an error term following $N(0,\sigma^2)$.

Analyses of the seasonal structure of pollinator assemblages. *Predicting species phenology in different locations and years.* To assess the effect of phenological shifts at the scale of the full pollinator assemblages, we calculated changes in the overlap among phenologies. As phenological shifts depend on location, we discretized the studied area in cells of 5°×5°. This size was chosen to smooth the differences in sampling effort among localities. To ensure a representative pollinator assemblage, we included only grid cells with at least 3 insect orders with 20 species with at least 30 records each. The remaining cells were considered as under-prospected. Thus, species are considered present in a grid cell if it has at least 30 records between 1960 and 2016. By doing so, we assume that the compositions of species assemblages are the same in 1980 and in 2016, which allows us to study only the effect of phenological shifts on seasonal structure. We considered that all species have the same abundance, and a circular Gaussian phenology. We used wrapped circular normal distributions instead of a classical Gaussian distribution to take phenologies that span winter into account. We estimated the mean and the standard deviation of these Gaussians for the years 1980 and 2016 and for each grid cell, using the predictions of the linear models used to estimate phenological shifts, described in equations (3) and (4).

Calculation of phenological overlaps within assemblages. For each sufficiently prospected grid cell, we calculated the pairwise overlap among the pollinator phenologies present in the given grid cell. We considered that all species have the same abundance, and a circular Gaussian phenology. The overlap between two phenologies is the integral of the minimum of both Gaussians. We calculated two overlap measures for each grid cell: the first one focusing on the overlap within insect orders and the other one among insect orders. To give equal weight to each

insect order, and thus avoid over-representation of Lepidoptera, we first calculated the mean overlap by insect order, or by pair of insect orders, respectively, for the overlap within and among orders. Second, we averaged these mean values per grid cell. Finally, to have more robust values, we repeated this overlap calculation after shifting segmentation of the latitude and the longitude by 1.25°, 2.5° and 3.75°. Then we averaged values obtained by 1.25°×1.25° grid cells for both measures, overlap within and among orders.

To study the seasonal dynamic of overlap changes, we calculated a proxy of the phenological overlaps day by day in 1980 and in 2016 for each grid cell (Extended Data Fig. 5). We did not use exactly the same calculation of overlap as previously for computational reasons. To simplify the calculation method, we aggregated predicted phenologies at the order level to get a density distribution by order, henceforth called order phenologies, as presented in Fig. 3a. Then we calculated the pairwise overlap among the order phenologies day by day for both years, 1980 and 2016, and for each grid cell. We also evaluated the day-by-day density value for each order phenology for both years, 1980 and 2016, and for each grid cell. This density value is a proxy of the phenological overlap within order, because we assume that every species has the same constant abundance. Then we calculated the daily changes of both these indices between 1980 and 2016 (Extended Data Fig. 5). We did so for only one grid pattern (that is, without sliding windows).

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The final dataset analysed in this paper is available at https://zenodo.org/record/3480120.

Code availability

The codes used to extract data from the GBIF, to separate modes of multimodal phenologies and to estimate phenological shifts are available at https://github.com/f-duchenne/Flower-visitors-phenology.

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Author contributions

F.D., C.F. and E.T. conceived the project. F.D. assembled the dataset and performed the statistical analysis. F.D., C.F., E.T., D.M. and M.E. interpreted the results. M.D., M.Persson, J.S.R.-P., M.Pollet and P.V. provided data and biological expertise on the studied species. F.D. wrote the paper with contributions from all authors.

Competing interests

The authors declare no competing interests.

Additional information

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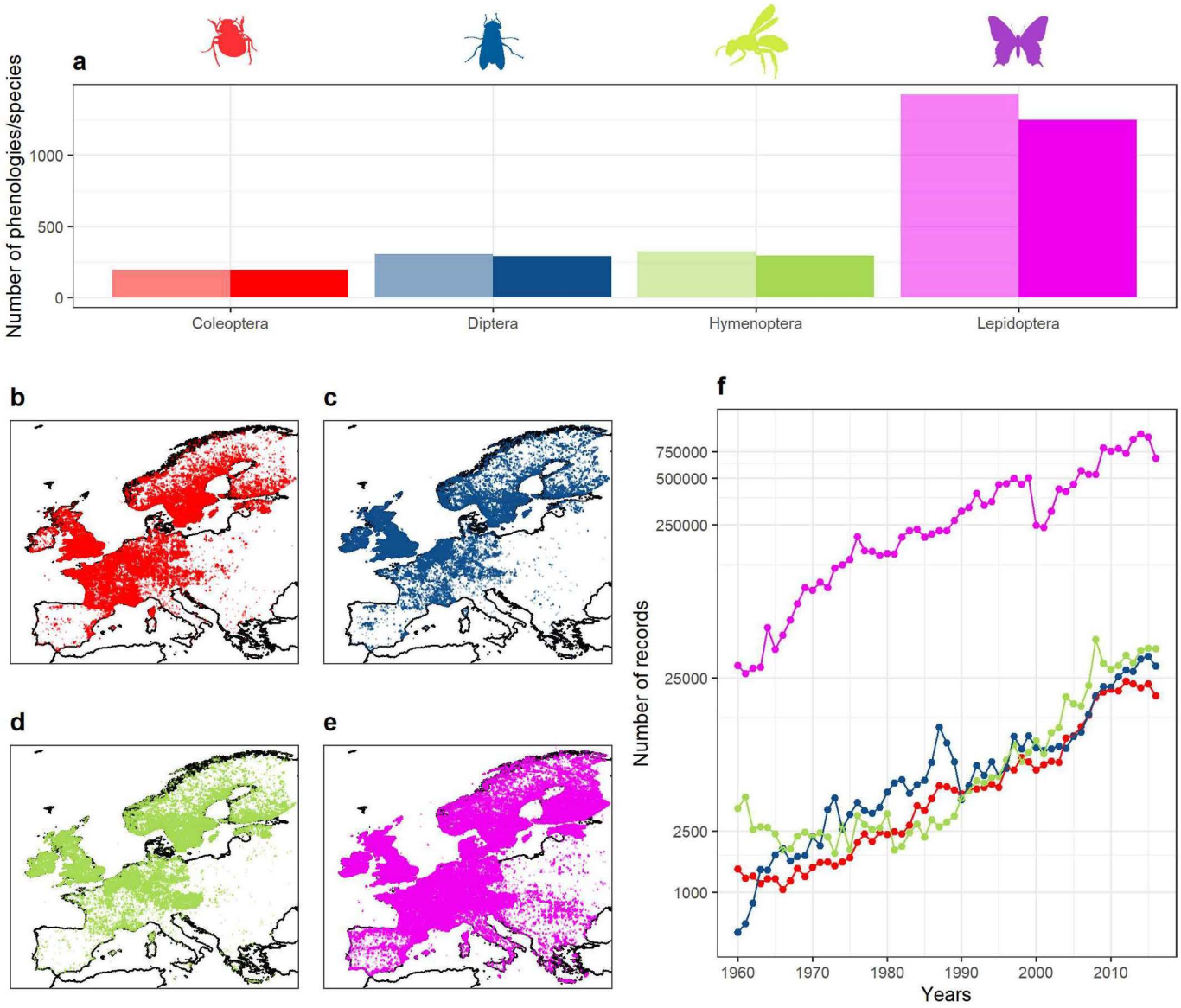
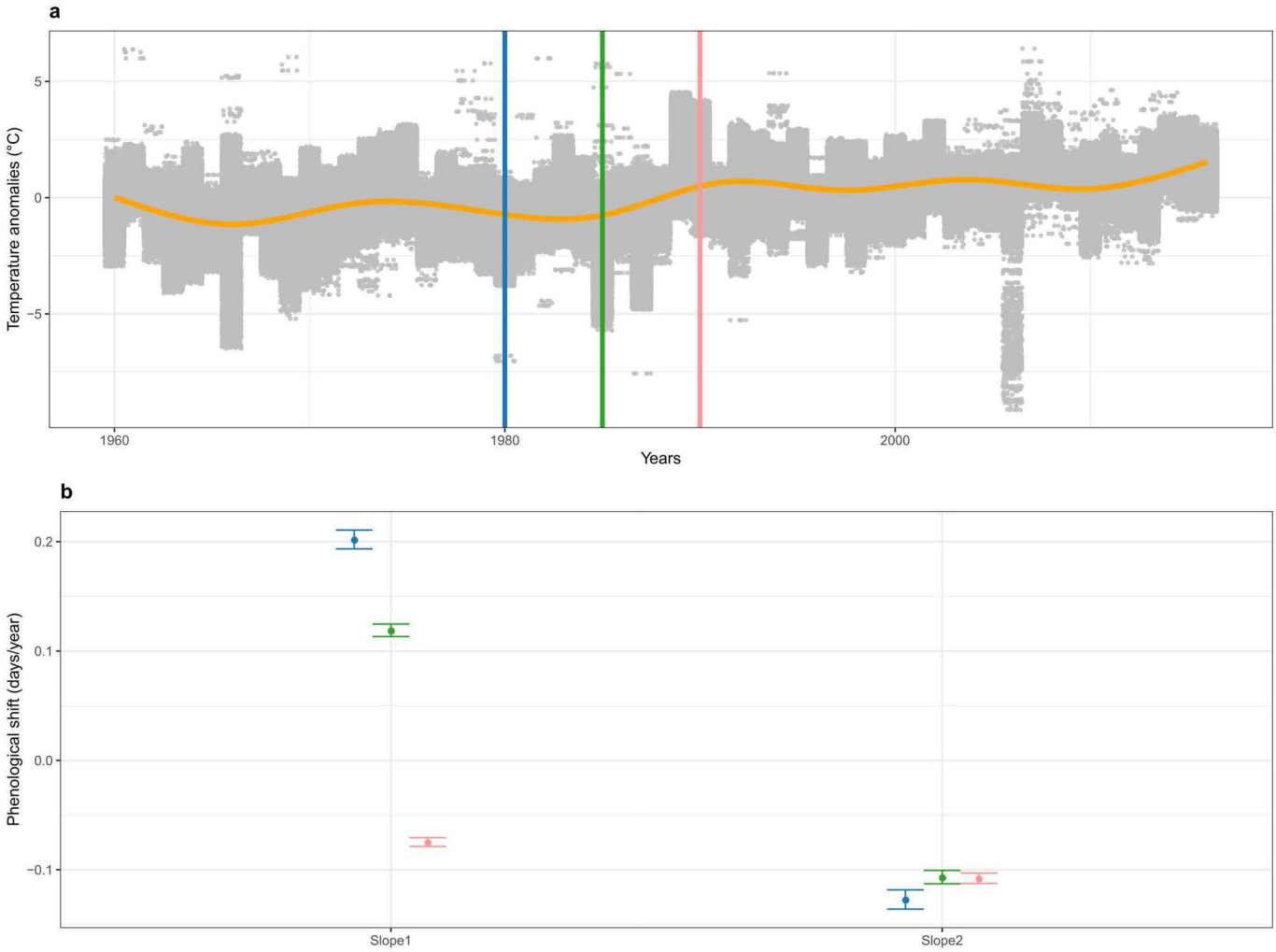
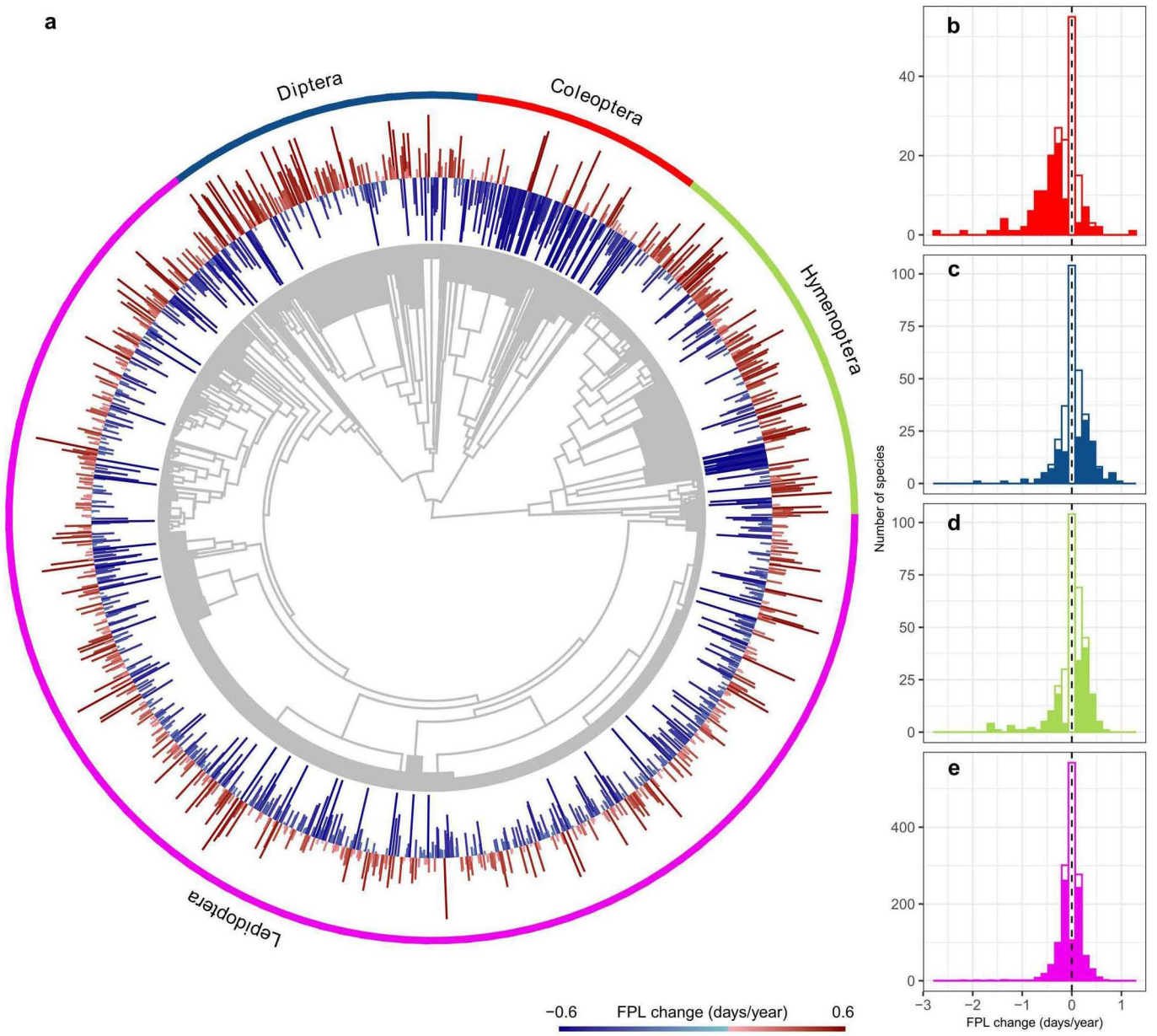


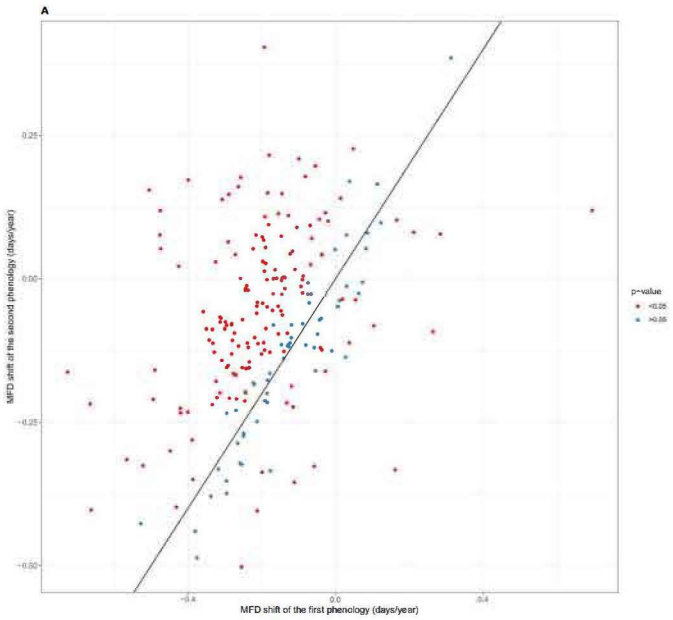
Extended Data Fig. 1 | Spatial and temporal distribution of records by order. a, Number of phenologies (light colors, left) and species (dark colors, right) for each insect order. **b-e**, Spatial and **f**, temporal distribution of records for Coleoptera (**b**, red), Diptera (**c**, blue), Hymenoptera (**d**, light green) and Lepidoptera (**e**, magenta). Y-axis of (**f**) is on a $\log_{10}$ scale.



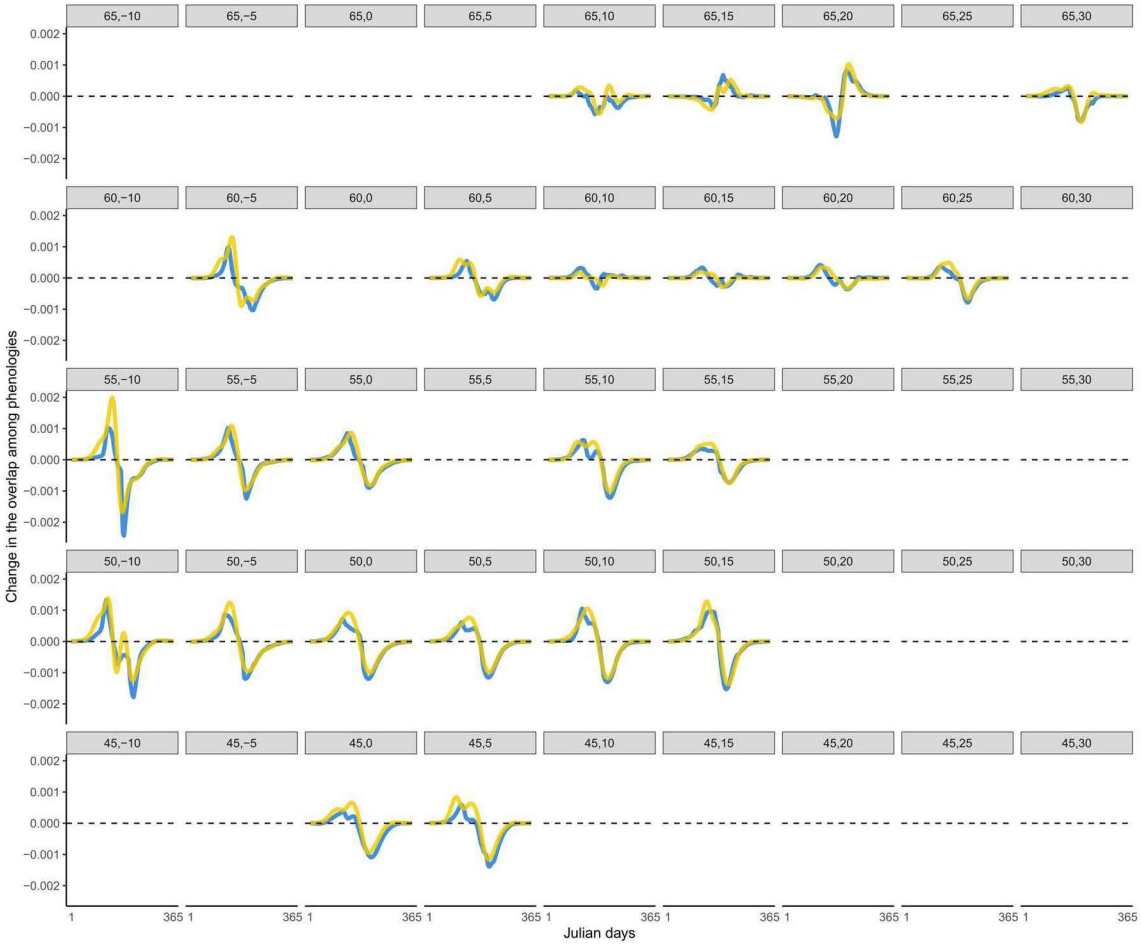
Extended Data Fig. 2 | Average MFD shifts before and after the temperature increase. a, Temperatures anomalies on the first 150 days of each year against years. The orange curve represents the result of a LOESS fit. Vertical lines show the position of the 3 breakpoints chosen to define periods used in (**b**). **b**, Mean flight date shifts for the whole pollinator assemblage by period, before the breakpoints (Slope1) and after the breakpoints (Slope 2).



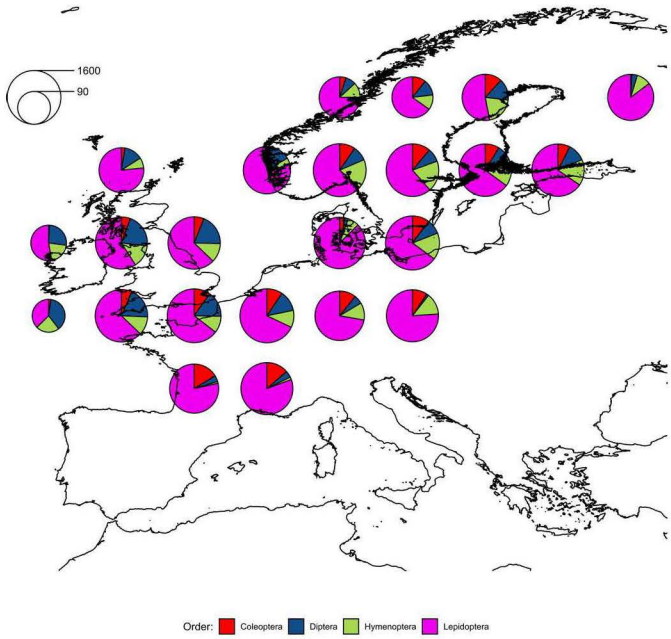
Extended Data Fig. 3 | Flight period length (FPL) changes of European flower visitors between 1960 and 2016. a, Phylogeny of studied species showing FPL shifts. The bars around the phylogeny tips are proportional to the FPL shifts and colored in blue and red for shortening and lengthening, respectively. Values are truncated to −0.6 and to 0.6 days/year to preserve readability. Histograms show FPL shifts for all studied species of **b**, Coleoptera (red), **c**, Diptera (blue), **d**, Hymenoptera (light green) and **e**, Lepidoptera (magenta). Full bars represent species with values significantly distinct from zero whereas open bars are species with a value non-significantly distinct from zero. FPL shifts shown here are predicted for the averaged latitude and longitude of each species' records.



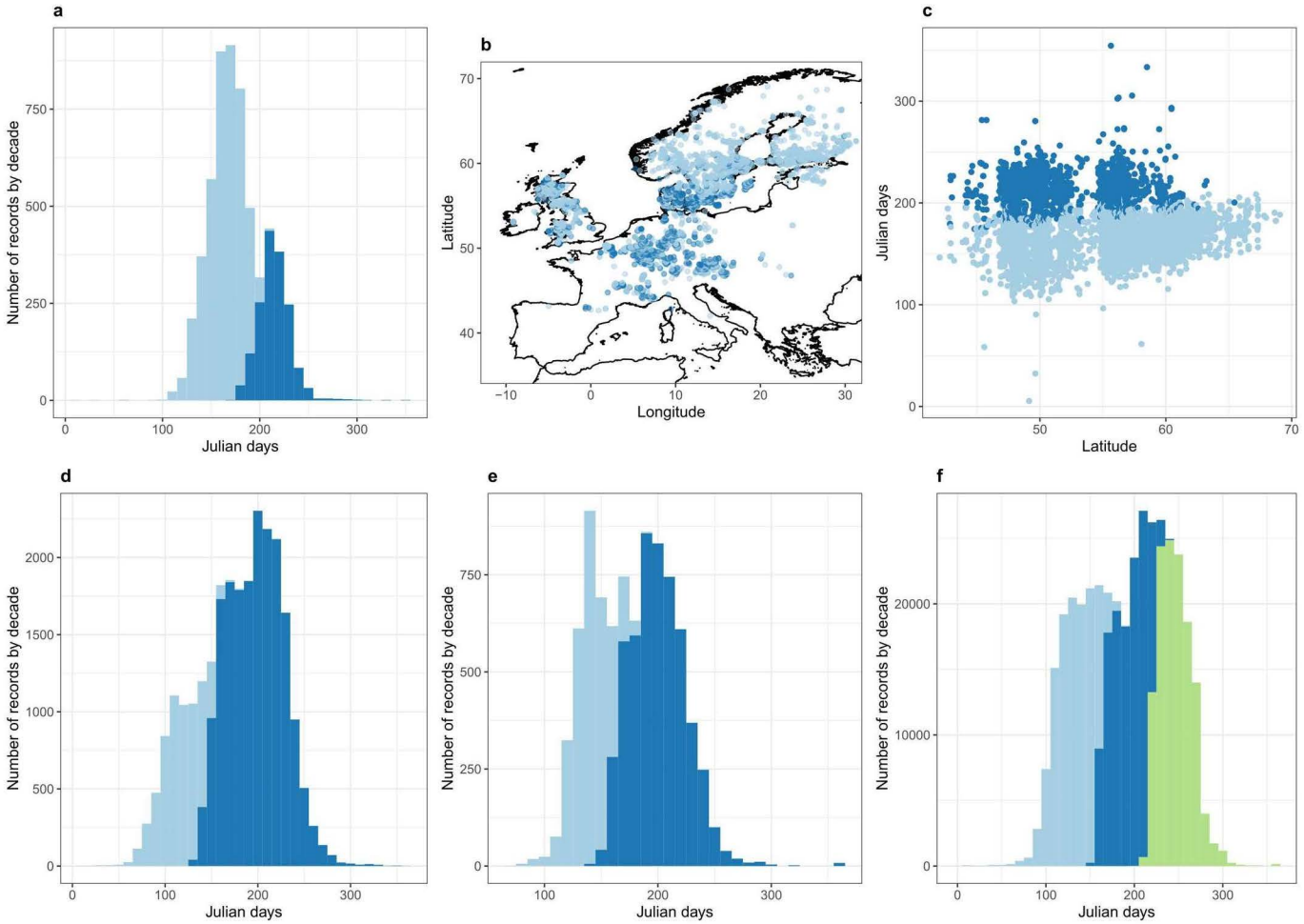
Extended Data Fig. 4 | MFD shifts of the second mode against MFD shifts of the first mode for multimodal phenologies. Mean flight date (MFD) shifts of the second mode against MFD shifts of the first mode for all 190 species presenting a multimodal phenologies with enough data in 2 modes to study both (cf. Methods). Color indicates p-value (red: <0.05 and blue >0.05) of the Z test comparing both shifts. The black line is the first bisector. Red points above the first bisector show species with a first mode advancing significantly more than the second one, while red points under the first bisector show the opposite pattern and blue points do not show any significant differences between two mode shifts.



Extended Data Fig. 5 | Seasonal changes in the overlap among phenologies between 1980 and 2016. Changes in the overlap among orders (blue) and within orders (yellow) between 1980 and 2016 along the season, considering only grid cells with enough data (see Supplementary Fig. 6). Cells are sorted by latitude then longitude (Lat,Long).



Extended Data Fig. 6 | Spatial distribution of phenologies in grid cells. Number of phenologies by order in 5° × 5° grid cells, considering only grid cells with enough data, that is with at least 3 insect orders including at least 20 species with at least 30 records each.



Extended Data Fig. 7 | Examples of multimodal phenologies split into distinct modes. The example of *Epirrhoe tristate* (Lepidoptera) shows how our method distributes records in function of **a**, Julian days, **b**, space and especially **c**, latitude. Other examples for *Bombus lapidarius* (**d**, Hymenoptera), *Melitaea phoebe* (**e**, Lepidoptera) and *Pararge aegeria* (**f**, Lepidoptera). For the *Bombus*, we can see that our method is able to separate emerging queens (light blue) and workers/males (dark blue) phenology, whereas we also detect 3 modes for *Pararge aegeria* and 2 for *Melitaea phoebe* in agreement with what we know about the voltinism of these species.

Appendix I_{bis}

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Author Correction: Phenological shifts alter the seasonal structure of pollinator assemblages in Europe

F. Duchenne, E. Thébault, D. Michez, M. Elias, M. Drake, M. Persson, J. S. Rousseau-Piot, M. Pollet, P. Vanormelingen and C. Fontaine

Correction to: *Nature Ecology & Evolution* https://doi.org/10.1038/s41559-019-1062-4, published online 23 December 2019.

In the version of this Article originally published, the name of author J. S. Rousseau-Piot was mistakenly written as J. S. Piot. This has now been corrected.

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Appendix II

Duchenne F., Thébault E., Michez D., Gérard M., Devaux C., Rasmont P., Vereecken N. J. & Fontaine C. Long-term effects of global change on occupancy and flight period of wild bees in Belgium. *Accepted in Global Change Biology*

Long-term effects of global change on occupancy and flight period of wild bees in Belgium

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Short running title: **Long-term effects of global change on bees**

Keywords: pollinator | phenology | abundance | community | urbanization | climate change | agricultural intensification

Statement of authorship: FD, ET, CD and CF designed the study. FD performed the statistical analyses. PR, NJV and DM provided distribution records, MG, NJV and DM provided species traits. FD wrote the paper with contributions from all authors.

Abstract

Global change affects species by modifying their abundance, spatial distribution and activity period. The challenge is now to identify the respective drivers of those responses and to understand how those responses combine to affect species assemblages and ecosystem functioning. Here, we correlate changes in occupancy and mean flight date of 205 wild bee species in Belgium with temporal changes in temperature trend and interannual variation, agricultural intensification and urbanization. Over the last 70 years, bee occupancy decreased on average by 33%, most likely because of agricultural intensification, and flight period of bees advanced on average by 4 days, most likely because of interannual temperature changes. Those responses resulted in a synergistic effect because species which increased in occupancy tend to be those that have shifted their phenologies earlier in the season. This leads to an overall advancement and shortening of the pollination season by 9 days and 15 days respectively, with lower species richness and abundance compared to historical pollinator assemblages, except at the early start of the season. Our results thus suggest a strong decline in pollination function and services.

Introduction

Global change drivers, such as climate warming, agricultural intensification and urbanization, strongly affect pollinators, decreasing their occupancy and advancing their flight periods (Bartomeus et al., 2011; Potts et al., 2010; Roy & Sparks, 2000). Because pollinators provide key ecosystem functions (Ollerton et al., 2011) and services (Klein et al., 2007), concerns about a pollination crisis have increased over the last decades (Potts et al., 2010). Lower pollinator occupancy and diversity can indeed translate into lower pollination performance (Biesmeijer et al., 2006; Potts et al., 2010), while shifts of flight periods can induce a temporal mismatch with their mutualistic partners (Gérard et al., 2020; Memmott et al., 2007). However, despite a sustained research effort on the topic, our understanding of both causes and consequences of the pollination crisis is still limited.

First, a good understanding of the mechanisms responsible for observed differences in species responses to global change is currently missing. Recent studies have shown that global change can drive species thrives or declines, making winner and loser species, respectively. Estimated occupancy trends for British pollinators over the last decades show that while populations of most species declined, populations of a few species increased (Powney et al., 2019). Similar heterogeneity holds for phenological changes: while most European pollinators advanced their flight period, some others delayed it or appeared unaffected (Duchenne et al., 2020). While heterogeneity in species response is often overlooked, a better understanding of it, in particular by studying species traits that could explain these distinctive responses, can provide insights on both the drivers and mechanisms impacting species (Biesmeijer et al., 2006).

Second, we still know very little about how different species responses, such as changes in pollinator occupancy and flight period, affect pollinator assemblages when they are combined. A pioneering study suggests that species persistence and phenology are not independent, as pollinators flying later in the summer have higher rates of extinction than do early-flying pollinators (Balfour et al., 2018). We also know that pollinators flying earlier in the season tend to advance more their flight period than do pollinators flying latter (Bartomeus et al., 2011; Duchenne et al., 2020). As a consequence, joint changes in occupancy and in flight period could affect the seasonal structure of pollinator assemblages, thereby altering pollination networks (Memmott et al. 2007, Encinas-Viso et al. 2012). The joint study of occupancy and phenological species responses is thus key to gain insights on how pollinator assemblages and related function and services are and will be affected by global change.

Finally, understanding of the respective impacts of several global change drivers on species also remains limited, due to a lack of long time series of protocoled data for many species and difficulties to disentangle the effects of correlated environmental changes. Long-term monitoring schemes only exist for a few groups of insects, such as butterflies (Pollard & Yates, 1994). For most species, the study of how each global change driver affects pollinator occupancy mainly comes from spatial comparisons among areas with distinct levels of disturbance (Pickett, 1989; Winfree et al., 2009). Spatial comparisons have shown that agricultural intensification decreases pollinator occupancy and richness (Grab et al., 2019; Kremen et al., 2002; Le Féon et al., 2010) but have yielded contrasting results regarding the effect of urbanization on pollinator occupancy or/and richness (Bates et al., 2011; Deguines et al., 2012; Fortel et al., 2014). However, space-for-time substitution often neglects local adaptation and site history, which can lead to opposite trends in spatial and temporal patterns (Adler & Levine, 2007; Isaac et al., 2011; White & Kerr, 2006). This stresses the need to study temporal series to unambiguously identify the drivers of temporal variations (Dornelas Maria et al., 2013). One potential source of long time series of data come from museum and private collections (Bartomeus et al., 2019). Such data are increasingly used to assess shifts in flight periods (Bartomeus et al., 2011; Hassall et al., 2017) or changes in occupancy of pollinators (Powney et al., 2019).

The drivers of temporal changes in species responses are difficult to identify because several drivers might exhibit correlated temporal trends but nonetheless can have independent impact on species responses. For example, climate warming, which is generally suspected to be driving the observed shifts in flight period of pollinators, correlates with urbanization that also affects the phenology of pollinator activity (Luder et al., 2018). Similarly, agricultural intensification and climate warming have been shown to affect the persistence of bumblebees (Goulson et al., 2008; Soroye et al., 2020) and they both increased in recent decades. This points out the importance of simultaneously testing several potential drivers if one wants to identify the main threats for pollination.

Here we tackled the three points presented above: (i) identify the species traits related to positive and negative occupancy and flight date shifts, (ii) assess how these species responses combine themselves thereby affecting wild bee assemblage, and (iii) quantify the independent effects of four global change drivers – i.e. agricultural intensification, urbanization, temperature trend and inter-annual temperature changes – on the shifts in species occupancies and species flight dates. We based our analysis on the estimation of the temporal trends in occupancy and mean flight date over the last 70 years for 205 bee species in Belgium, using relevant statistical

methods to correct bias associated with historical opportunistic data, such as temporal variations in sampling pressure and temporal autocorrelation. By investigating these three points using a unique dataset, we show how several drivers of global change affect biodiversity from individual species to species assemblage and discuss associated risks for the related function and services.

Material and methods

Methods overview

Our goal was threefold: (1) estimate temporal trends in occupancy and flight date of numerous bee species as well as identify traits related to the variation among species, (2) quantify the changes in the seasonal structure of the bee assemblage between 1950 and 2016, and (3) estimate the independent effects of global change drivers on occupancy and mean flight date over the last 70 years. The first step, common to the three goals, consisted in computing unbiased national and annual estimates of occupancy and mean flight dates from historical data (Fig. 1). For the first goal, we estimated linear temporal trends of occupancy and mean flight date and we identified species traits associated with those trends, while controlling for species phylogenetic dependence (Fig. 1). For the second goal, we combined the annual estimates of occupancy and mean flight date to reconstruct the seasonal structure of the bee assemblage by decades (Fig. 1). For the third goal, we correlated yearly changes in occupancies and mean flight dates with yearly changes in the four potential drivers (Fig. 1), i.e. agricultural intensification, urbanization, temperature trend and inter-annual temperature changes. Analyzing yearly changes decreases the expected correlation among potential drivers and their correlation with time (Fig. S1), allowing a better insight into the size effects of the potential drivers on the species responses.

Dataset and species selection

Records of bees from Belgium were compiled from the database *Banque de Données Fauniques de Gembloux et Mons*. This dataset contains about 269,000 records from 1810 to 2017, for 412 bee species within or at the margins of Belgium (Table S1; Fig. S2). Here we used occurrence records, constituted by a species name, a sex, a date of collection, and a location, providing latitude, longitude and elevation. Because we want to estimate flight period shifts and occupancy trends over a period relevant for the study of the effects of global change and because bee records from the first part of the century are sporadic, we trimmed the dataset to restrict it to records pertaining to the period 1950-2016, and retained wild bee species with

at least 30 records for the 1950-2016 period and spread all along the time period studied: with more than one record before 1980, between 1980 and 1990 and after 1990. These filtering steps led to a dataset of 179,948 records belonging to 205 wild bee species (Fig. S2).

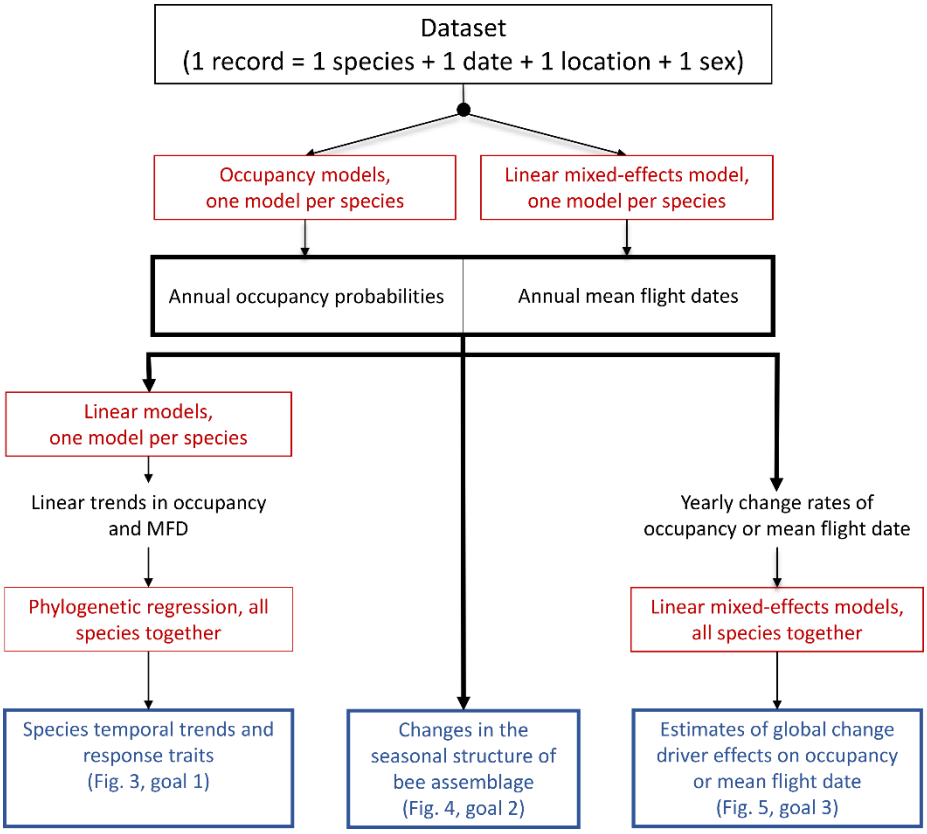

Figure 1: *Statistical steps applied on the bee dataset. Red boxes correspond to statistical models, black text to raw data or intermediate estimates and blue boxes to the goals. MFD stands for mean flight date.*

Annual estimates of occupancy probability and mean flight date

We estimated a national mean flight date (MFD) for each year of the time period and each bee species using the occurrence data. We used the predictions from a linear mixed-effects model for each species to get mean flight date estimates that account for variations in space and time of collection location. This model explains variation in the collection dates of a bee species by a polynomial relation with year, to model the temporal trend of mean flight date, and by latitude, longitude and altitude to account for collection location. We also added a random year effect, to account for inter-annual variation in mean flight dates, and a random sex effect to control for its expected effect. For some records, information about the sex was missing and thus inferred (cf. supplementary method 1).

$$FD_{ijs} = \beta_0 + \beta_1 \times years_j + \beta_2 \times years_j^2 + \beta_3 \times years_j^3 + \beta_4 \times latitude_i + \beta_5 \times longitude_i + \beta_6 \times altitude_i + \varphi_j + \theta_s + \varepsilon_{ijs} \quad (1)$$

where FD_{ijs} is the day of the year of observation *i* belonging to sex *s* and year *j*, β_0 is the intercept, β_1, β_2 and β_3 are polynomials coefficients of the year effect, β_4, β_5 and β_6 are the respective coefficients for latitude, longitude and altitude effects. φ_j and θ_s are random year and sex effects respectively, and finally ε_{ijs} is an error term; random terms are all expected to be independent, identically distributed, and homoscedastic.

We used the Bayesian method from Powney et al. (2019) to get estimates of national and annual probabilities of occupancy for each species separately. Such method, developed for opportunistic data, accounts for temporal variation in detection probability, thereby taking into account changes over time in the species targeted by collectors. This method also infers non-detection events, as required for opportunistic data. We aggregated records spatially using a grid cell with a cell size of 0.01° of latitude/longitude and temporally by the day of the year, excluding grid cells with data from a single year. We defined a species detection in a given grid cell and day as the collection of the targeted species at this location and date. Conversely, we defined non-detection for a species in a given grid cell and a given day as the absence of the targeted species while at least another wild bee was collected at this location and date. We used the following occupancy model independently for each species:

$$\textbf{State model}: z_{ij} \sim \text{Bernoulli}(\psi_{ij}) ; logit(\psi_{ij}) = b_j + u_i \quad (2)$$

$$\textbf{Detection model}: y_{ijv}|z_{ij} \sim \text{Bernoulli}(z_{ij} \times p_{ijv}) ;$$

$$logit(p_{ijv}) = \alpha_j + \delta \times \log(NS_{ijv}) + \gamma_3 \times \frac{1}{\beta_2 \times \sqrt{2\pi}} e^{-\frac{(\text{FD}-\gamma_1)^2}{2\gamma_2^2}} \quad (3)$$

where z_{ij} is the true (unknown) status of the species (0 absent or 1 present) and ψ_{ij} is the probability of occupancy of grid cell *i* at year *j*, and which is modelled as a fixed year effect b_j and a random grid cell effect u_i. y_{ijv} represents the detection status for the same species (1 or 0) at grid cell *i*, year *j*, and visit *v* defined by the collection date. p_{ijv} is the estimated probability of detection at grid cell *i*, year *t* and visit *v*, is conditional upon $z_{ij} = 1$ and modeled as a random year effect α_j, accounting for variation in detectability among years. δ is the effect of the sampling effort, approximated by the logarithm of the number of species (NS_{ijv}) detected in the cell *i* on year *j* and visit *v* . Because we log transform the number of species collected, this effect captures whether during a visit, one, few or more species were detected, which mainly depends on the sampling pressure and not so much on the species richness of the site which should be

captured by the grid cell effect u_i (Isaac et al., 2014). γ_1, γ_2 and γ_3 are effects of the day of the year of the visit (*FD*), with a bell-shaped function modelling the flight period.

We fitted the occupancy model for each species separately using the *Sparta* R package (Isaac et al., 2014), with 2 chains, 50,000 iterations, a burnin of 35,000 and a thinning rate of 3. We used the random walk half-cauchy prior formulation used by Outhwaite et al. (2018), which improves the convergence of the models. For some species the convergence was not good enough (less than 60% of occupancy estimates with Rhat<1.1). For these species, we used 65,000 iterations with a burnin of 50,000. To estimate the annual proportion of Belgium occupied a given year by a given wild bee species, i.e. occupancy, we averaged its predicted presences (z_{ij}) over all grid cells for the corresponding year. Occupancy measured as such reflects the abundance of a species, due to the close relationship between both (He & Gaston, 2003).

Finally, the national annual mean flight date estimates correspond to the predictions from the equation (1), for the average longitude, latitude and altitude of records of the corresponding bee species, while annual occupancy probabilities correspond to the predictions from equation (2), averaged over all grid cells.

Goal 1: temporal trends and correlation with species traits

To asses if we could identify species traits related to the changes in species occupancy and mean flight date, we first estimated linear temporal trends for occupancy and mean flight date, and this for each species independently. To do so, we regressed annual occupancy and mean flight date estimates on years, accounting for the precision of the estimates by weighting them by the inverse of their associated standard errors and considering only years with records to estimate mean flight date temporal trend.

Second, we built a database of species traits derived from collection materials, literature and data analyses based on our database and the European records of Hymenopterans from GBIF. This database is complete for 200 species (Supplementary Method 2, Table S3). We also built a phylogeny including 203 wild bee species (Supplementary Method 3). Overall, this led to 199 bee species with complete trait data and included in the phylogeny. We considered species traits that have already been documented as correlated to either changes in occupancy/abundance or mean flight date shifts: mean flight date over years (Bartomeus et al., 2011), flight period length (Bartomeus et al., 2013), species temperature index, measured by the average temperature preference of a species (Bartomeus et al., 2013), species continentality index, measured by the variability of the climatic conditions experienced by a species through its geographic range

(Rasmont et al., 2015), intertegular distance as a proxy of bee size (Bartomeus et al., 2013), overwintering location (Williams et al. 2010), sociality (Williams et al. 2010; Powney et al. 2019), pollen diet generalism, i.e. polylectic vs oligolectic (Bartomeus et al., 2013; Williams et al., 2010). Details on these traits can be found in the Supplementary Method 2.

Finally, we explained linear temporal trends in occupancy and mean flight date with species traits, using a phylogenetic generalized least squares model (PGLS) implemented in the *caper* R package (Orme et al. 2013), controlling for the Pagel's λ at the maximum likelihood, a robust measure of phylogenetic signal (Pagel, 1999). We first checked for collinearity problems in the model by calculating a generalized variance inflation factor, and because we did not get values upper to five, we then used a backward selection of variables based on AIC. We removed traits one by one to get the lowest possible AIC value and we stopped to remove species traits from the model when it was not possible to decrease the AIC anymore.

Goal 2: Consequences for the seasonal structure of the wild bee assemblage

To assess how changes in occupancies and mean flight dates affect the species assemblage, we reconstructed the seasonal structure of the wild bee assemblage, at national scale, for each decade of the studied period. To do so, for each species and decade, we first modeled the flight phenology as a Gaussian curve, with the mean corresponding to the average of annual mean flight date estimates over the decade and standard deviation (i.e. flight period length) corresponding to the standard deviation of the date of flight records (i.e. Supplementary Method 2). Thus, we assumed that species flight period length was constant over decades, which is verified for 93% of the species, but are different among species.

Second, to account for variation in occupancy among species and decades, we multiplied each Gaussian, which estimates the phenology of a species at a given decade, by the respective occupancy calculated as the average of annual occupancy probability estimates over the decade and species of interest. This gave us the daily occupancies of each species in each decade.

Finally, for each decade, we summed over all species and separately for each day of the season these species daily occupancies, thereby obtaining the daily total occupancy of the pollinator assemblage throughout the season. We then characterized the seasonal structure of wild bee assemblages by its peak date and duration, calculated as the number of days with daily total occupancy of the pollinator assemblage above 0.01 or 0.05. We also calculated the daily species richness for each decade, as the number of species with a daily occupancy probability above 0.002.

To evaluate the respective contribution of changes in occupancy and mean flight date to changes in the phenological structure of the wild bee assemblage, we also reconstructed the daily total occupancy of the pollinator assemblage when only considering changes in occupancy (keeping MFD constant, with the species values from 1950) or only considering changes mean flight date (keeping occupancy constant, with the species values from 1950).

Goal 3: identifying the global change drivers of species responses

We focused on agricultural intensification, urbanization and temperature changes as potential drivers of changes in occupancy and mean flight date of bees. Data on these drivers were extracted at the country level (i.e. national average value) for the period 1930-2016. These drivers are all strongly correlated with time, and consequently among them, and cannot be used in the same statistical model. We instead analyzed the relationship between yearly changes in occupancy and mean flight date and yearly changes in global change drivers. Indeed, the yearly changes in the drivers are less correlated with time and among them than raw values (Fig. S1), allowing to better untangle the respective effects that each potential driver have on occupancy and mean flight date. Finally, as we expected the drivers to affect differently the bee species, especially those with declined *vs* increased occupancy over years or those with advanced or delayed mean flight dates over years, we divided the bee species into groups of increasing, decreasing or stable occupancy, and independently into groups of advancing, delaying or stable mean flight date.

Data on global change drivers

For the climatic driver of global change, we used the mean annual temperature over Belgium from the Brussel-Uccle observatory. As temperature exhibits both a trend and strong inter-annual variability, both of interest, we split these data into two variables: one describing the trend, which corresponds to temperatures smoothed over time, and one describing the inter-annual temperature changes, and which simply corresponds to raw temperature data. To obtain the temperature trend, we smoothed temperature data using a Locally Estimated Scatterplot Smoothing (LOESS), with a span parameter of 0.5. Note that results shown below are robust across a wide window of smoothing parameter values (Fig. S5).

We based our proxy of agricultural intensity on mean wheat yield, as previously done (Donald et al., 2006; Storkey et al., 2012), extracted from the World in Data (https://ourworldindata.org). Annual wheat yield depends on both agricultural practices and climatic conditions. To remove the effect of inter-annual climatic variability and focus on the long-term trend of wheat yields, which is mainly related to agricultural intensification (Zhai et

al., 2017), we smoothed the annual mean wheat yields using LOESS with a span parameter of 0.5 (Fig. S4).

We based our proxy of urbanization on the total built-up area in Belgium, which was extracted from the HYDE database V3.2 (Goldewijk et al., 2011). The total built-up area in Belgium was available every 10 years before 2000 and every years after 2000. As total built-up area in Belgium is not expected to show any inter-annual variations around the trend, we interpolated missing data using a LOESS with a span parameter of 0.2 (Fig. 2).

From time series to yearly changes

Once the time-series were obtained for the four components of global change, we computed their yearly changes ΔD_j by taking the difference between year *j* and *j-1* for each variable *D*, and scaled that difference with the standard deviation of the ΔD time series. Standardizing ΔD_j allows providing the same potential effect of each driver of global change on the response variables. Those yearly changes in the global change variables correspond to the global change drivers.

In a similar way, we computed the yearly change for species *k* from year *j-1* to year *j* in occupancy or mean flight date, $\Delta_{O_{jk}}$ and $\Delta_{MFD_{jk}}$, from the logit of the annual occupancy probabilities (O) and mean flight dates (MFD). To account for estimation errors, for each variable *X*, occupancy or mean flight date, we combined the standard errors of the two years used to calculate that of the yearly changes as follow: $SE_{\Delta Xj} = \sqrt{SE_{j-1}^2 + SE_j^2}$. To compute those yearly changes, we used only occupancy rates that converged well (Rhat<1.1) and mean flight date predicts corresponding to years with records of the given species. Moreover, since some occupancy yearly changes exhibit a very high associated standard error, we removed all $\Delta_{O_{jk}}$ with a standard error ≥30 (n=409 on 9541) to avoid including very uncertain data in following analysis. In the same way, we removed the few mean flight shifts with an absolute value ≥50 days (n=41 on 6842), because it is very unlikely they occurred between two consecutive years and more likely were produced by mistakes in collection dates.

Testing for the effects of global change drivers

We expected distinct effects of global change drivers on species depending on their responses. For example, we expect agricultural intensification to affect differently bees that exhibit a decrease in occupancy from those exhibiting an increase. We thus classified bee species in three groups according to their temporal linear trends in occupancy: significantly increasing species (winners), significantly declining species (losers) and stable species for those

with non-significant temporal trend. Similarly for the mean flight date, we split species into three groups according to their temporal linear trends: advancing, delaying and unaffected species.

We tested for the effect of scaled yearly changes in the four drivers of global change (ΔD_j), i.e. agricultural intensification (A), urbanization (U), temperature trend (TT) and inter-annual temperature changes (ITC), on yearly changes in occupancy Δ_O and mean flight date Δ_{MFD}. We built two independent linear mixed models accounting for species groups and their interaction with the drivers. We added a random species effect to take into account that all species do not have the same number of Δ_O or Δ_{MFD}, and a Ornstein–Uhlenbeck covariance structure to take into account temporal autocorrelation. We included only wild bee species for which at least 25 yearly changes could be calculated (n=168 for occupancy, n=128 for mean flight date):

$$\Delta_{X_{kgj}} = \beta_{0_g} + \beta_{A_g} \times \Delta\mathrm{A}_j + \beta_{\mathrm{ITC}_g} \times \Delta\mathrm{ITC}_j + \beta_{TT_g} \times \Delta\mathrm{TT}_j + \beta_{U_g} \times \Delta\mathrm{U}_j + \varphi_{j_{(k)}} + \varepsilon_{kgj} \quad (4)$$

Where $\Delta_{X_{kgj}}$ are the yearly changes in variable *X* (O or MFD) of the species *k* belonging to the group *g*, on the year *j*. β_{0_g} is the intercept, β_{A_g}, β_{TT_g}, β_{ITC_g} and β_{U_g} are standardized effects of the drivers, depending on the group *g* of the species. $\varphi_{j_{(k)}}$ is a year random effect depending on the species *k* used to implement the Ornstein–Uhlenbeck covariance structure. ε_{kgj} is the error term, expected to be independent, identically distributed and homoscedastic. We implemented the model using the R package *glmmTMB* (Brooks et al., 2017). To account for statistical uncertainties, yearly changes were weighted in the model by the invert of their standard errors. For occupancy these weights were elevated at power 0.2, to avoid very heterogeneous weights leading to convergence problems. We also checked for collinearity among variables by calculating a variance inflation factor values for global change drivers. We did not get values above five, suggesting that collinearity among driver should bias estimates.

Results

Species responses

Across all bee species over 1950-2016 in Belgium, occupancy and mean flight date yearly estimates reveal that the occupancy decreased on average by about 33% (Fig. 2a) and that bees were active earlier, on average, by about 4 days (Fig. 2b). Linear trends in occupancy per species indicate that distributions have shrunk for 125 "loser" species (61%) whereas 30 "stable" species (14%) did not exhibit any significant change, and 50 "winner" species (24%) had increased their distribution areas (Fig. 3a, Table S4). Turning to flight period, we find a significant linear advancement of the mean flight date for 83 species (40%), 96 species (47%) were unaffected and 26 species (13%) delayed their mean flight dates (Fig. 3a, Table S4). Note that over the 1950-2016 period, global change accelerated, as shown by the trends in the four potential drivers tested here (Fig. 2c).

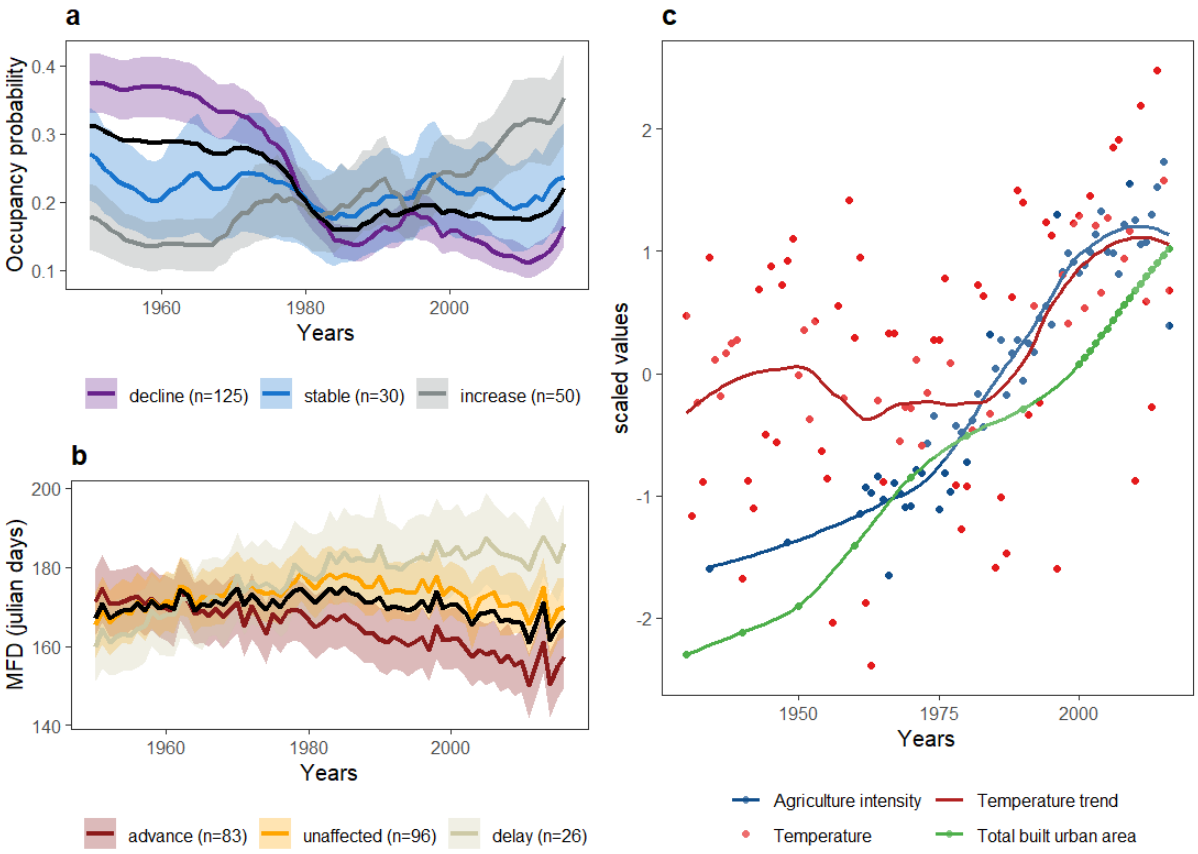

***Figure 2:* Occupancy and mean flight dates changes over time and trends in global change variables.** *Predicted variation of (a) occupancy probability and (b) mean flight date (MFD) across years averaged by species groups, and their associated $CI_{95\%}$ interval represented by ribbons. Black lines represent the average value over all species. (c) scaled (centered by mean and scaled by standard deviation) values of the global change variables (circles) and values used to calculate drivers (lines).*

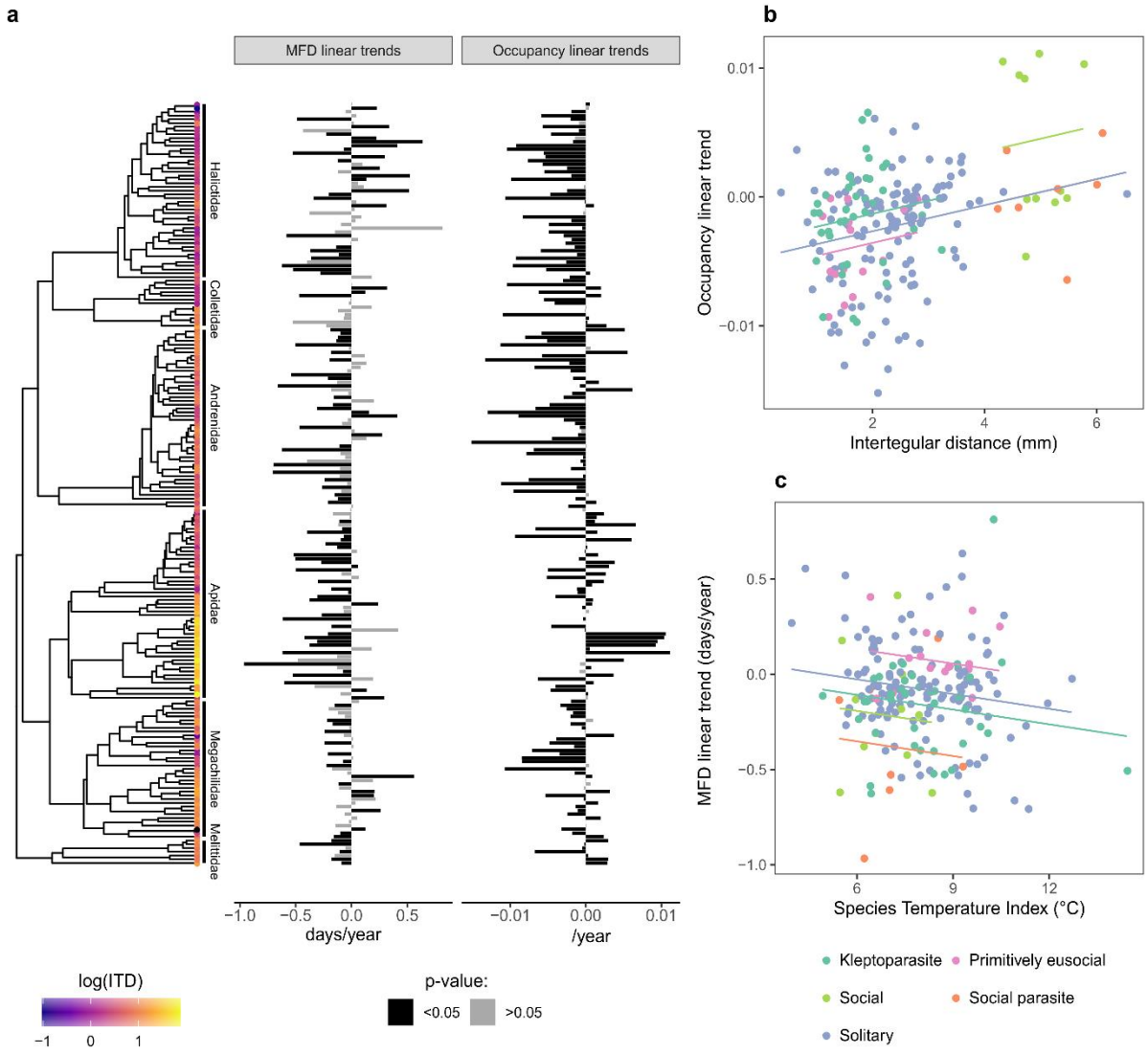

***Figure 3:* traits related to the linear temporal trends in occupancy and mean flight date (MFD) over the study period.** *(a) Relationships among phylogeny, bee size measured as intertegular distance (ITD) and temporal linear trends in occupancy and mean flight date, for the species included in the phylogeny (n=203). Intertegular distances are represented by the leaf color of the phylogeny. Black leaf represent the species with no value of intertegular distance (n=1). Black bars represent significant trends while grey bars represent non-significant trends. (b) Relationships among intertegular distance, sociality behavior and occupancy trends (n=199). (c) Relationships among species temperature index, sociality behavior and mean flight date linear trends (n=199). Lines represent the prediction of the Phylogenetic Generalized Least Squares regressions. Values of mean flight date shifts and occupancy trends are shown in Table S4.*

Correlation between species responses and species traits

We find that several species traits correlated to species responses. The social behavior of bees is associated with both the occupancy and mean flight date linear trends over years, with social bee populations declining less and advancing more their flight date than primitively eusocial and solitary ones (Fig. 3, Table 1). The thermal niche of species is also related to the linear trends in mean flight date, with southern species advancing more their flight period than

do northern ones (Fig. 3c). Finally, we find that bee size is strongly correlated to the occupancy linear trends, with larger species decreasing less their mean occupancy than smaller ones (Fig. 3b, Table 1), this effect remaining significant when excluding bumblebees, which are especially large species (Table S5).

We find a significant phylogenetic signal in the occupancy linear trends over time (Table 1), indicating that global change affects some clades of bees more strongly, thereby increasing the loss of phylogenetic diversity. On average, Halictidae (-0.0036 ± 0.0005 $year^{-1}$) and Andrenidae (-0.0034 ± 0.0007 $year^{-1}$) are the most declining families while Melittidae (0.0002 ± 0.001 year-1) and Apidae (0.0008 ± 0.0006 year-1) slightly gained in occupancy over time. Such phylogenetic signal is likely due to strong links between occupancy trends and phylogenetically conserved traits, like bee size (Fig. 3a), as this phylogenetic signal disappears when accounting for the effect of response traits (Table 1). We do not find any significant phylogenetic signal in mean flight date linear trends (Table 1).

Table 1: *Estimates, standard errors and p-values for both Phylogenetic Generalized Least Squares models (PGLS) explaining linear trends in occupancy trends and mean flight date (n=199). NA (non-attributed) values indicate that the selection based on the AIC removed this trait for this response. Pagel's λ values included in the PGLS (taking into account species trait effects) and rough Pagel's λ values (without taking into account species trait effects) are indicated. Pagel's λ equal to zero means that there is no phylogenetic signal, while a value significantly different from zero means that there is a phylogenetic signal.*

		MFD linear temporal trends			**Occupancy linear temporal trends**		
		Estimate	**SDE**	**p-value**	**Estimate**	**SDE**	**p-value**
Species Temperature Index		-0.02579	0.01154	0.02657	0.00035	0.00019	0.06671
Sociality (ref=Kleptoparasite)		-	-	0.0001	-	-	0.0257
	Social parasite	-0.24401	0.10322	-	-0.00134	0.00219	-
	Solitary	0.08148	0.04577	-	-0.00135	0.00083	-
	Primitively eusocial	0.24119	0.07704	-	-0.00226	0.00128	-
	Social	-0.08412	0.08660	-	0.00280	0.00195	-
Mean flight date		0.00010	0.00106	0.04933	NA	NA	NA
ITD		NA	NA	NA	0.00101	0.00040	0.01222
Pagel's λ (PGLS)		0.00; $CI_{95\%}$[0.00,0.08]			0.02; $CI_{95\%}$[0.00,0.18]		
Pagel's λ		0.10; $CI_{95\%}$[0.00,0.34]			0.21; $CI_{95\%}$[0.07,0.44]		

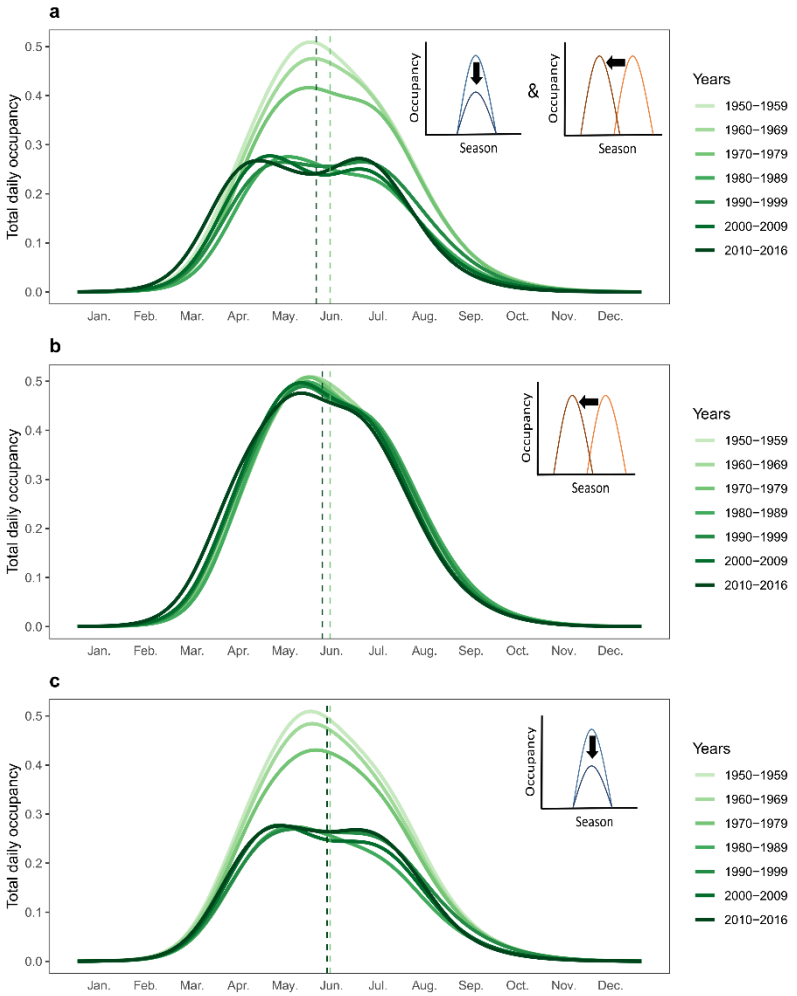

Figure 4: ***Seasonal variations of the total occupancy of pollinators over decades***. *(a) Reconstruction considering both occupancy and MFD changes, (b) reconstruction considering only MFD shifts, historical occupancy being fixed over decades, and (c) reconstruction considering only occupancy changes, historical MFD being fixed over decades. Dashed vertical lines represent the weighted mean of the seasonal total occupancy distribution for 1950-1959 (light green) and for 2010-2016 (dark green).*

Consequences of occupancy trends and mean flight date shifts on the bee assemblage

The temporal linear trends in mean flight date and occupancy were negatively correlated (r=-0.14, p-value=0.04, Fig. S6): species that show an increase in occupancy probabilities over time tend to advance their mean flight date, while those that show a decrease in occupancy tend to delay their mean flight date. By reconstructing the seasonal structure of bee assemblages throughout the study period using yearly estimates of occupancy and mean flight date, we show that this correlation between the two species responses resulted in a synergistic effect on the seasonal structure. The peak of total daily occupancy is 8.97 days earlier in the recent decade compared to 1950-1960 when both occupancy and mean flight date changes are considered (Fig. 4a), while it is 5.05 days earlier when only mean flight date changes are taken into account (Fig. 4b), and 1.87 days earlier when only occupancy changes are considered (Fig. 4c). The predicted additive effect of changes in mean flight dates and occupancy thus corresponds to a

peak earlier by 6.92 days, which remains below the predicted change when both species responses are studied jointly. Overall, the average season date has advanced by about 9 days between 1950 and 2016 (Fig. S6), while season length has shortened by about 15 days (Fig. S7a). We also observe a shift from a unimodal distribution in 1950 to a bimodal distribution of bee total occupancy and species richness in 2016 (Fig. 4a & S7b). All along the season excepting at its early beginning, the total occupancy and the richness of wild bee in present time is lower than in 1950.

Drivers of bee decline and flight period shifts

To investigate the potential drivers of each species response, we correlated the yearly changes of occupancy and mean flight date to the scaled yearly changes of drivers of global change, allowing for differences among groups of species. Winner, stable and loser bee species all benefited from temperature increase, their occupancy being positively and consistently correlated to temperature trend (Fig. 5a). Agricultural intensification and urbanization correlated negatively with the occupancy yearly changes of declining bees but not with the ones of stable or increasing species (Fig. 5a & Table S5). Note that the effect size (estimates) of urbanization on loser species is smaller than that of agricultural intensification; changing the smoothing parameter for the urbanization affects the estimates of urbanization (Fig. S5). As a consequence, agricultural intensification was most likely the main driver of the decline of wild bee species in Belgium over the last 70 years. Inter-annual temperature changes did not significantly correlate with occupancy yearly changes (Fig. 5a, Table S6), indicating that it is not a main driver of wild bee occupancy in Belgium..

Surprisingly, changes in mean flight date were solely explained by inter-annual temperature changes, bees being active earlier in warmer years, although not significantly for bees that delay their mean flight date (Fig. 5b, Table S7). Temperature trend, urbanization and agricultural intensification did not show correlation with mean flight date shifts (Fig. 5b).

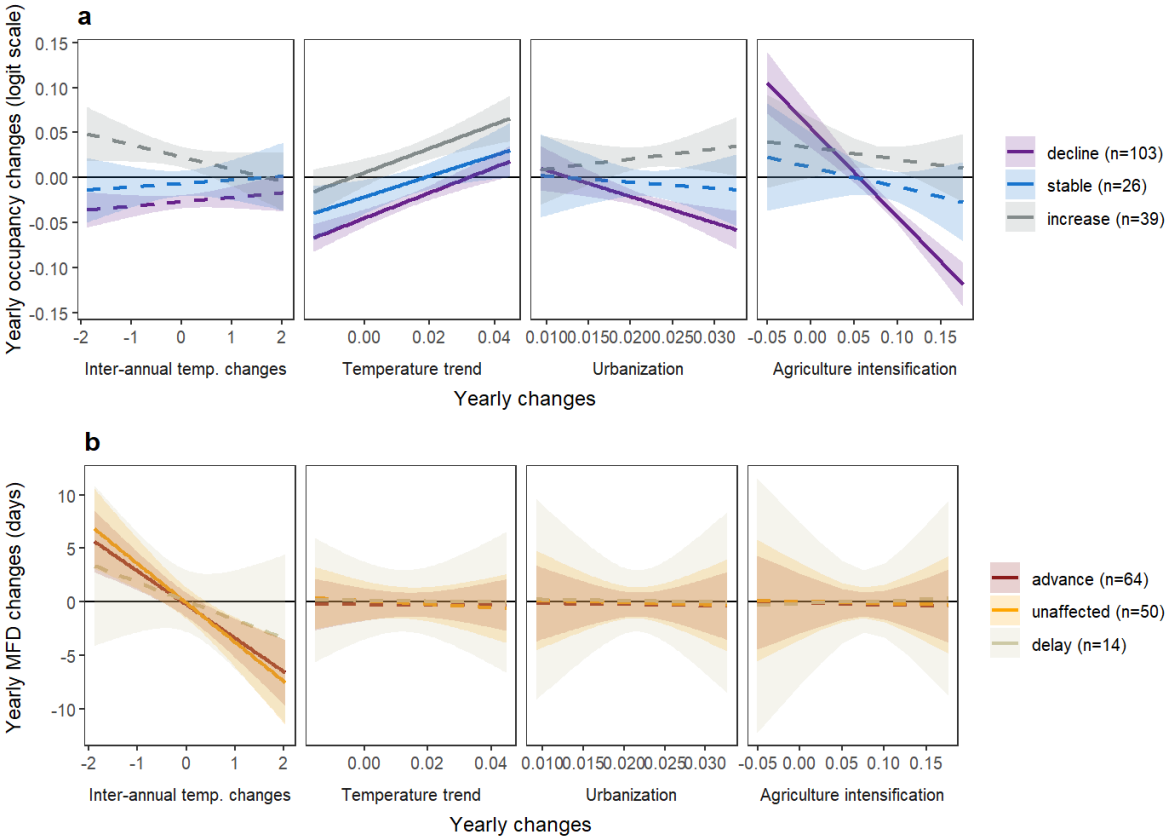

Figure 5: ***Drivers of occupancy and mean flight date (MFD) yearly changes depending on species group regarding their temporal linear trends for occupancy and MFD.*** *(a) occupancy yearly changes and (b) mean flight date yearly changes against yearly changes of global change variables, previously scaled (divided by standard deviation). The lines show the mixed-effect model predictions with their standard errors (ribbon). Dashed lines represent slopes that are non-significantly different from zero and solid lines represent slopes significantly different from zero.*

Discussion

Changes in wild bee assemblage over time

Our analyses indicate that 61% of the wild bee species declined and 40% advanced their mean flight date over the last 70 years. These patterns are consistent with the few studies using time-series to describe European bee population trends (Ollerton et al., 2014; Powney et al., 2019), and mean flight date shifts (Bartomeus et al., 2011; Duchenne et al., 2020). The negative correlation between the linear trends over years of occupancy and mean flight date is also consistent with previous results (Balfour et al., 2018), and suggests that these two types of responses jointly contribute to the shift towards early dates of the bee assemblage in average. Our analysis cannot disentangle whether this negative correlation results from a causal relationship or from the fact that both species responses are linked to bee social behavior. A causal link from phenological shifts to species persistence via trophic mismatch is sometimes suggested (Hegland et al., 2009). Such causal relationship is not supported by our data as the

bee decline occurred mainly before the shifts in flight periods. However, bee decline could also prevent shifts in flight period, since a strong decline in the population size can decrease the ability to respond to an environmental change because of expected decreased adaptive potential (Willi et al., 2006).

Such correlation between changes in occupancy and mean flight date led to synergistic effects on the seasonal structure of the pollinator assemblage, with the peak of total occupancy happening earlier than expected from additive effects of each response. This exemplifies how studying multiple species responses can benefit our understanding of the consequences of global change. Coupled with the overall decrease in occupancy along the season, such modifications of the seasonal structure of bee assemblage should lead to a decline in pollination function and services, especially for late flowering plants and crops. Studies on plant communities suggest that global change also affects the seasonal structure of flowering (CaraDonna et al., 2014; Diez et al., 2012), which can lead in some cases to a shift from unimodal to bimodal distributions of flowering abundance over the season (Aldridge et al., 2011), mirroring the pattern we find. However, these studies have been so far restricted to local American plant communities and thus cannot be directly compared to our results at national scale, stressing the need to investigate the interplay between the changes in seasonal structure of plants and pollinator communities.

Drivers of bee occupancy changes

Our study shows that the decline of bee populations was likely driven by land-use change, mainly agricultural intensification, and most likely not by climate change. This result is consistent with the negative effect of agricultural intensification found in studies based on spatial comparisons (Grab et al., 2019; Kremen et al., 2002). Agricultural intensification includes many variables that could have a negative effect on bee occupancy. The fact that bigger bees decline less than did smaller ones, could support the main role of two variables already documented having a negative effect on bees: pesticides (Goulson et al., 2015; Park et al., 2015) and habitat destruction (Park et al., 2015). Bigger bees have a higher physiological resistance to pesticides (Rafael Valdovinos-Núñez et al., 2009; Uhl et al., 2016) and higher dispersal abilities and foraging distance (Greenleaf et al., 2007), allowing them to suffer less from agricultural intensification than smaller bees. Another interpretation of social and big bees suffering less from agricultural intensification could be that they are especially targeted by conservation plans in agricultural landscapes in Europe (Nieto et al., 2014). However, our results regarding the positive relationships between body size and occupancy trend strongly

contrast with previous results, which found that larger bees are more prone to decline than smaller ones (Larsen et al., 2005; Rader et al., 2014; Scheper et al., 2014). These differences could emerge because we accounted for changes in detection probabilities over time while previous temporal studies did not (Scheper et al., 2014), which can bias occupancy trends (Isaac et al., 2014).

We also find that urbanization significantly discriminates between losers and winners of global change, suggesting that loser species suffer from urbanization while winners do not. This is consistent with the fact that those winners, social and big bees, are more present in urban area than solitary bees (Baldock et al., 2015). However, as we use national average time series, neglecting spatial heterogeneity of global change drivers and responses, we are not able to test that the occupancy increase of winners occurs mainly in urban areas. This stresses the need to use spatio-temporal partitioning of the respective role of global change drivers in species responses, but that requires finding massive historical time series of data, which are almost nonexistent for pollinators.

Our analysis further reveals that climate warming had a positive impact on bee occupancy in Belgium, even for declining bees. Such positive impact can be mediated by direct effects on wild bee physiology, as in temperate areas ectotherms are living in a climate cooler than their physiological optima in average (Deutsch et al., 2008), but also by indirect effects through changes in resource availability (Ogilvie et al., 2017). However, climate change could ultimately have an overall negative effect on bees as it involves other aspects than climate warming, such as extreme events, which have been shown to drive bumblebee decline (Soroye et al., 2020).

Drivers of mean flight date shifts

We do not detect any effect of the tested global change drivers on mean flight date other than the effect of inter-annual temperature changes. Large inter-annual temperature increases induce large changes for earlier mean flight date and vice-versa. This suggests that such response could be due to the high phenotypic plasticity of insect flight period (Sgrò et al., 2016), which allows fast responses to inter-annual temperature changes. However, we do not find any driver explaining the delay of the mean flight date that occurred for some species. This delay might be related to a more specific temperature index, for example an increase in winter temperature can delay bee emergence (Fründ et al., 2013). Also, we did not account for time-lagged responses in our analyses, while some responses to changes in drivers could occur years after and for a long time. For instance, changing competition pressures along the season because

of abundance changes could drive changes in mean flight dates (Rudolf, 2019), including delays for some species. Assessing simultaneously effects with and without time lags would require further methodological developments, but it is a key future step to understand well the effects of global change on biodiversity.

Methodological limits and perspectives

The effects of global change drivers tested here explain only a small part of the variance of changes in occupancy and mean flight date, 3% and 5.5%, respectively. This is likely due to several limits of our analysis. First, we looked for effects at the group level, thereby neglecting heterogeneity of response among species within groups. Second, we neglected the spatial heterogeneity in the global change drivers and species responses by analyzing changes at national level. This most probably lower the part of variance explained but it allows highlighting general patterns over time. Third, as previously mentioned we neglected time lags in the effects of global change drivers. Instead, we focused on breaking inevitable temporal correlations among global change drivers and time, and decided to limit our study to instantaneous effects only. For example, if agriculture intensification stops, our approach assumes that it has no more effect on bees, species response to perturbation can take years to occur, such as extinction and decline (Kuussaari et al., 2009), and bees could still decline because of high past level of agriculture intensity. Therefore, part of the unexplained variance in the response variable is most probably due to time-lag effects neglected here.

Despite such limits, our study reports an unprecedented quantitative estimation of the contributions of four global change drivers on the average decline and flight period shifts of pollinators over time. We show that the land-use changes were most likely the main drivers of pollinator decline over the last 70 years in Belgium. Such results can probably be generalized to a large part of Western Europe, where global change drivers are following the same trend as in Belgium.

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Supplementary Method 1: *Inferring the sex when it's missing*

In our database, 53007 records (28.3%) have no information about the sex of the individual. For these records, we inferred the sex before estimating phenological shifts. To do so, we used a random forest classification algorithm as implemented in the R package *randomForest*. We used full records (i.e. records with sex and date) as the learning bank (71.7% of the records), and we predicted the sex of the 28.3% of records without any information on the sex. On the learning bank, we got 16% of errors in the sex prediction, almost every times when there was no phenological differences among sex.

Supplementary Method 2: *Species traits database*

Species traits are listed in Table S2 as well as the corresponding variable types and data sources. Most traits were derived either from collection material (e.g. ITD) or from literature (e.g. sociality) as detailed in (Gérard *et al.* 2018). Additionally, for each species we calculated proxy of the mean flight date and of the flight period length, using respectively the mean and the standard deviation of the Julian day of all records from our dataset. We also calculated two temperature indexes. To do that we used the European records from GBIF of Hymenoptera (GBIF Occurrence Download, extracted on the 07 September 2018 https://doi.org/10.15468/dl.92odzl). We aggregated records spatially using a grid cell with a unit cell size of 0.01° of latitude and longitude. For each grid cell we got two bioclimatic variables from Bioclim (http://www.worldclim.org/bioclim): the annual mean temperature and the temperature seasonality, both averaged on the period 1970-2000. Then we calculated a species temperature index (STI) and a species continentality index (SCI) which are the average of each grid cell temperature and seasonality, respectively, weighted by the number of records of the species divided by the number of records of hymenoptera in the given cell.

Supplementary Method 3: *Developing a phylogeny of studied bees and phylogenetic analysis*

We constructed a bee phylogeny including all studied species but *Andrena sabulosa* and *Andrea varians*, as no sequence was available for these two species. We extracted Cytochrome c oxidase I (COI) sequences for each species from GenBank (Tab. S5). Phylogeny reconstruction used a relaxed-clock Bayesian approach implemented in Beast v1.5.4 (Drummond & Rambaut 2007). We constrained several sets of species that correspond to well-supported clades in two recent higher level phylogenies (Cardinal *et al.* 2010; Peters *et al.* 2017) (constrained nodes are indicated on Fig. S2). Using *PartitionFinder* (V. 2.1.1) (Lanfear *et al.* 2017), we found the best substitution model for each codon position. We used a pure birth tree prior and random starting tree and a GTR + Γ substitution model with invariant sites for the two first positions of codons. We assumed that substitution rate heterogeneity was lognormally distributed and uncorrelated, with the mean substitution rate set at 1. We conducted four runs of 20 million generations, sampling from the posterior distribution every 1000 generations. We built a maximum clade credibility tree from the last 10000 samples of the posterior distribution (Figure S2).

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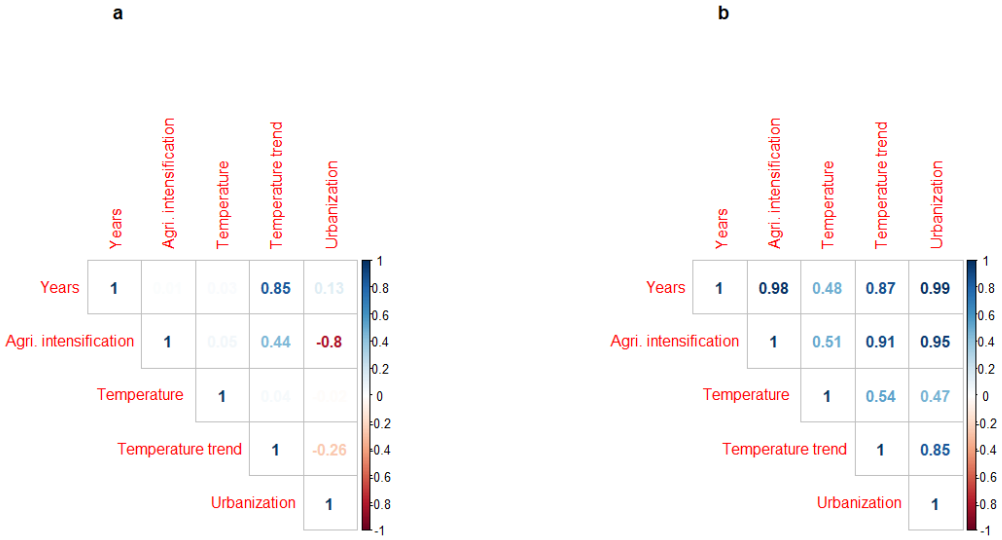
Table S1: Data providers of the *Banque de Données Fauniques de Gembloux et Mons*. A record is defined by a sampling event of one or several individuals at a given site (i.e. grid cell) and date.

Type of database	Number of records
BDFGM (Rasmont P. & Haubruge E.)	127,779
Waarnemingen.be/observations.be	122,708
DEMNA (Wallonia)	6,959
UFZ (Warncke)	6,393
RBINS	3,529
UGMD (Universiteit Gent)	1,058
UNamur	230
NMR (Netherlands)	298
Total	**268,954**

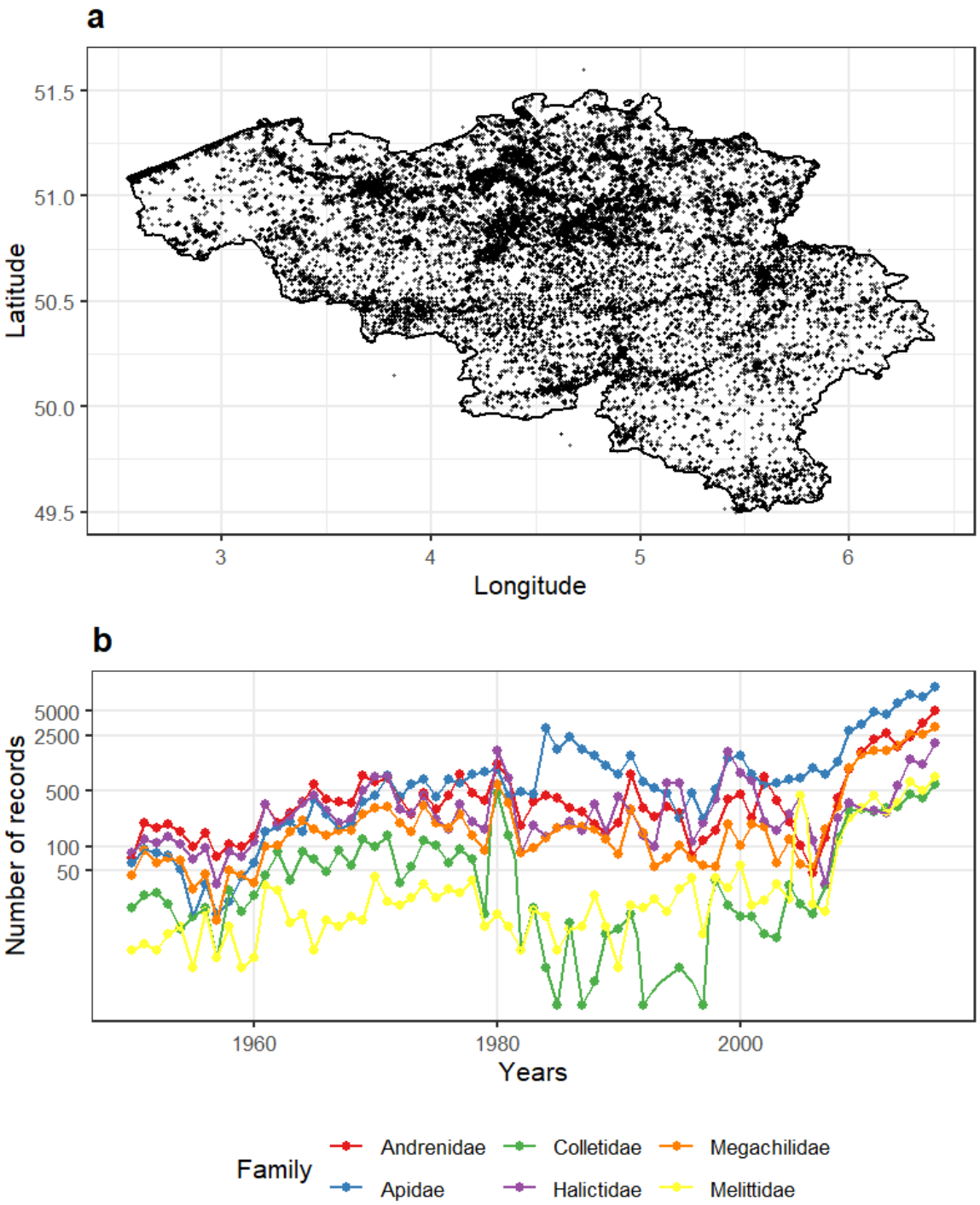
Table S2: species traits used in the study.

Species trait	origin	type
Mean flight date	Calculated from dataset	quantitative
Flight period length	Calculated from dataset	quantitative
Species Temperature Indices	Calculated from GBIF dataset	quantitative
Species Continentally Indices	Calculated from GBIF dataset	quantitative
Overwintering location	Gérard *et al.* 2018	qualitative (2 levels: above ground / under ground)
Sociality	Gérard *et al.* 2018	qualitative (5 levels: Social / Social parasite / Kleptoparasite / Primitively eusocial / Solitary)
Generalist/specialist	Gérard *et al.* 2018	qualitative (2 levels: Oligolectic / Polylectic)
Intertegular distance (ITD)	Gérard *et al.* 2018	quantitative

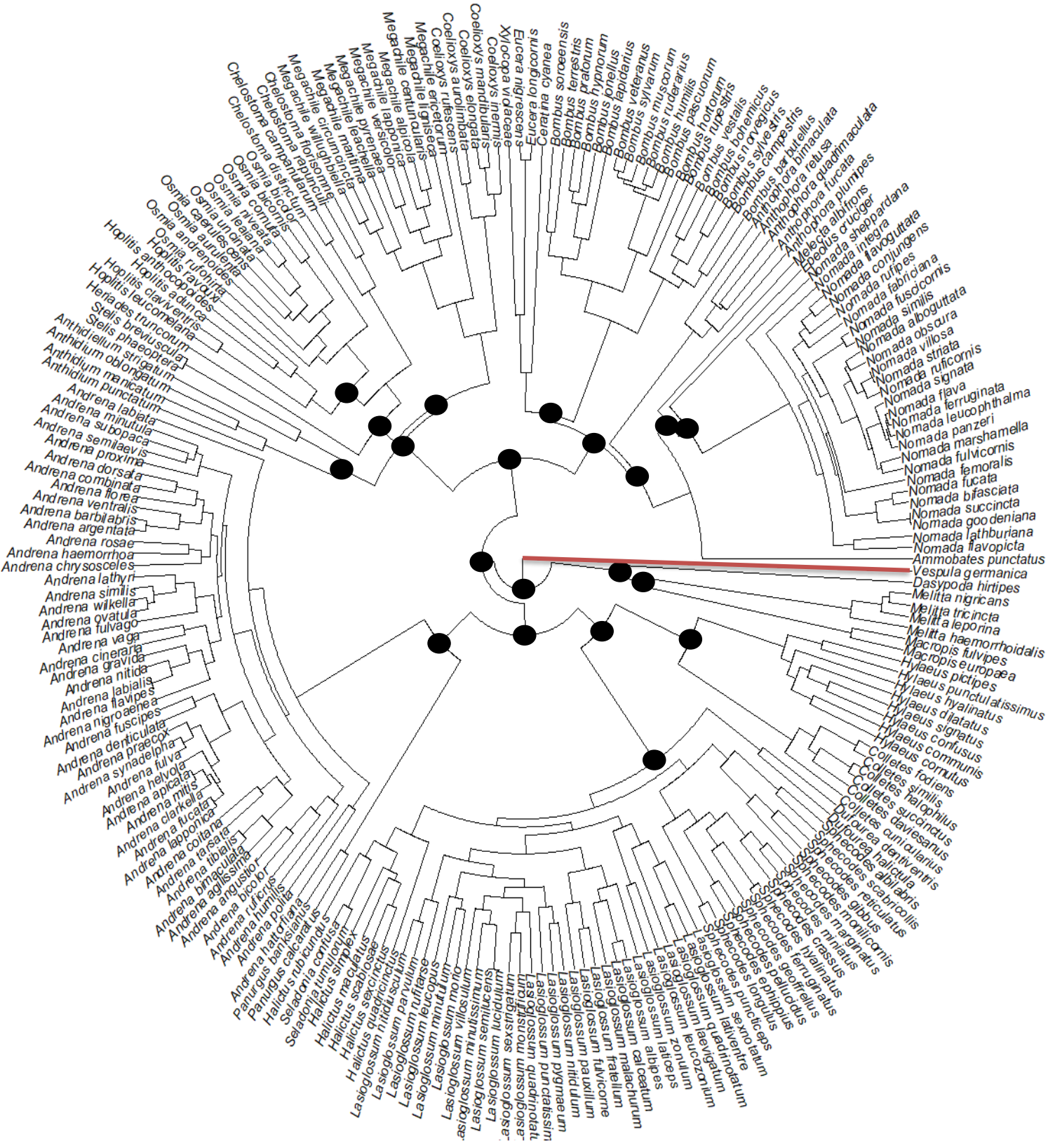
<u>Figure S1:</u> Correlations among drivers and their yearly changes on 1950-2016. (a) Correlations among yearly changes of global change drivers and with time. (b) Correlations among raw values of global change drivers and with time. This figure shows that working on yearly changes allows decreasing temporal correlations among global change variables.



<u>Figure S2:</u> Spatial and temporal distributions of records. (a) Spatial distribution of records used for analyses, (b) temporal distribution of these records by bee families.



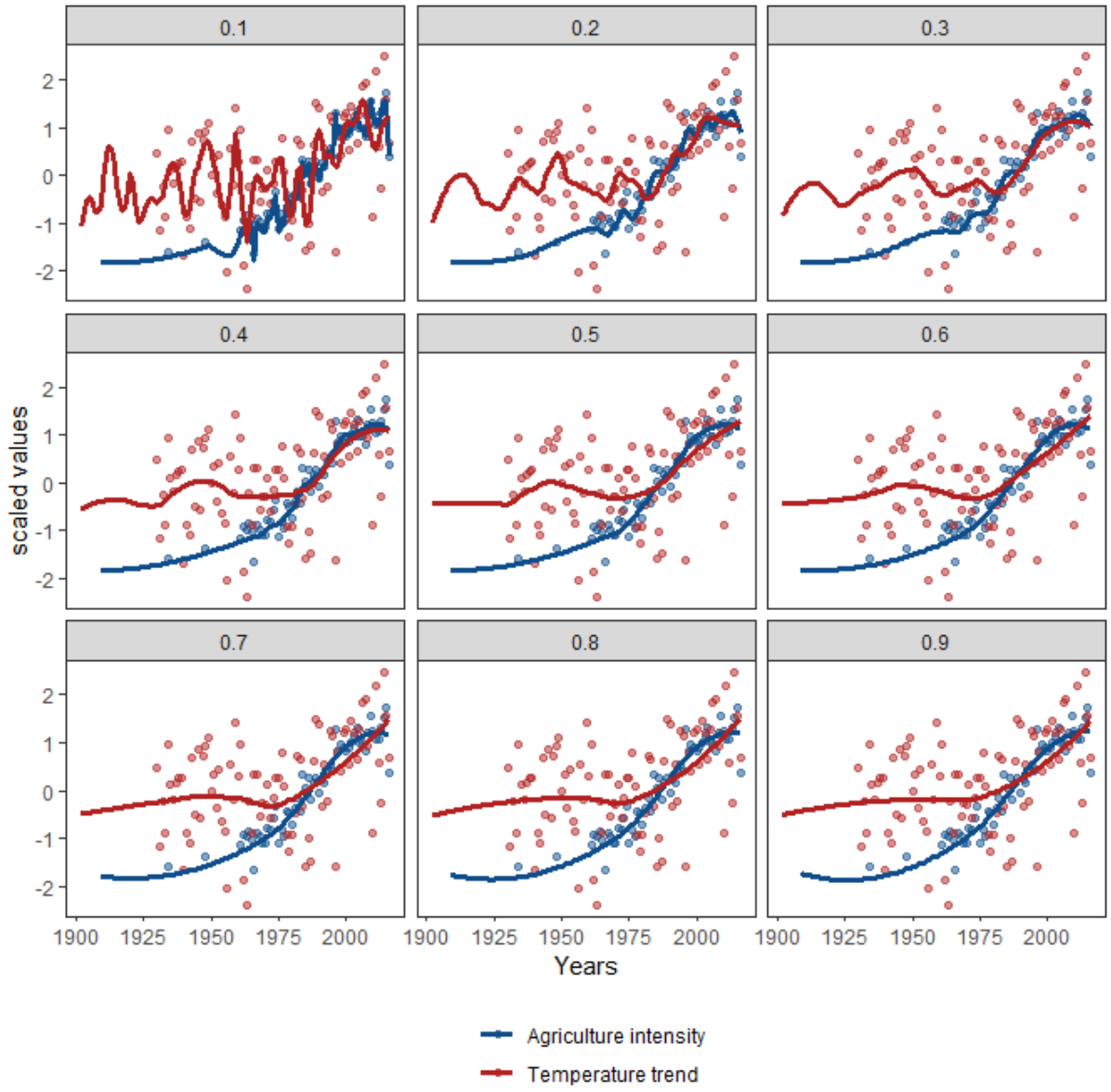
<u>Figure S3:</u> Phylogeny of the bees with *Vespula germanica* as outgroup. Constrained nodes (see methods) are indicated by filled circles. The orange branch represents the outgroup branch. *Bombus terrestris* corresponds to *Bombus terrestris sensu lato*.



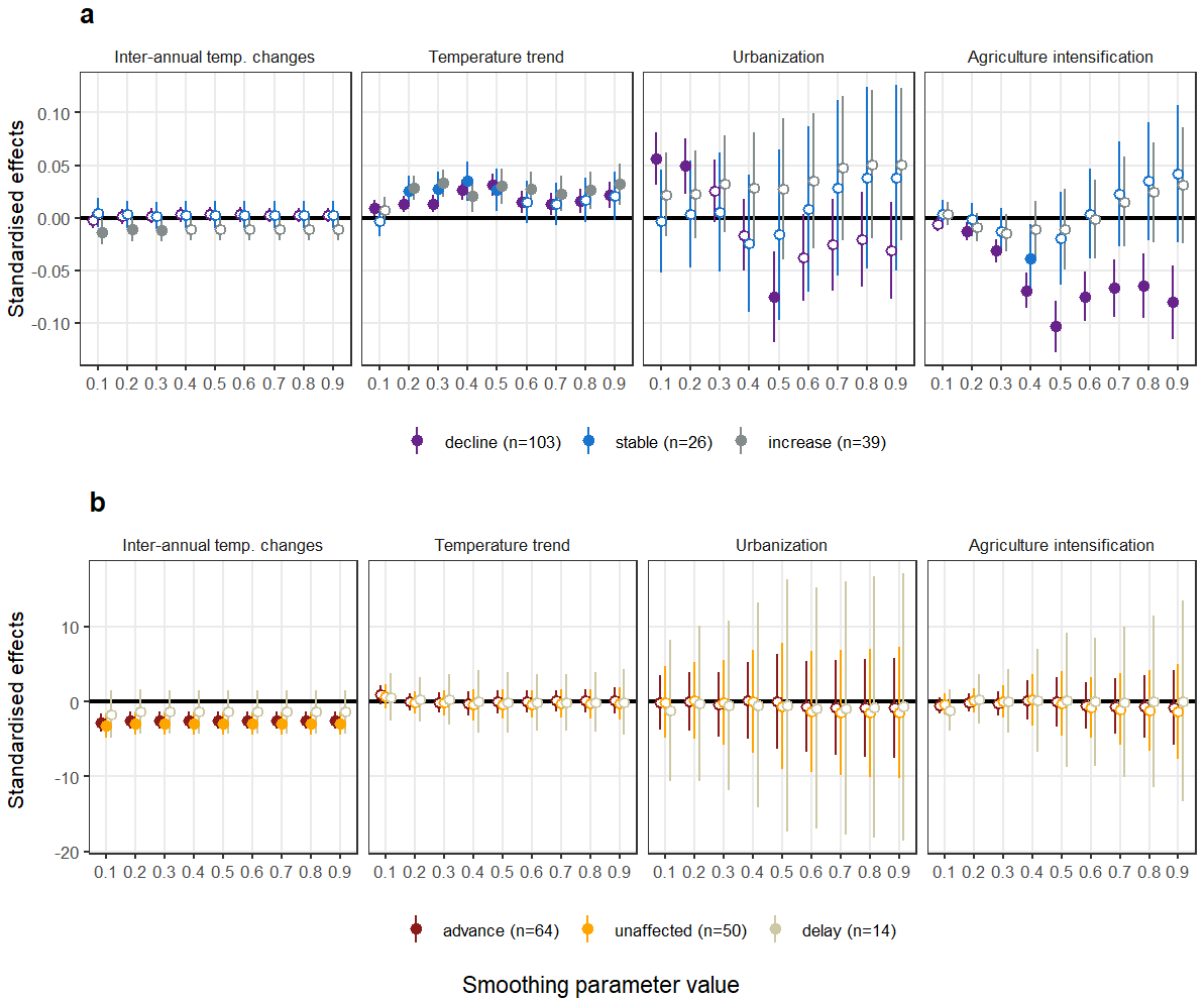
<u>Table S5:</u> Estimates, standard errors and p-values for both Phylogenetic Generalized Least Squares models (PGLS) explaining linear trends of occupancy trends and mean flight date when exlucding Bombus (n=181). This table is similar to the Table 1 of the paper, but when Bombus are excluded to analysis. NA (non-attributed) values indicate that the selection based on the AIC removed this trait for this response. Pagel's λ values included in the PGLS (taking into account species trait effects) with 95% confidence interval. Pagel's λ equal to zero means that there is no phylogenetic signal, while a value significantly different from zero means that there is a phylogenetic signal.

		MFD linear temporal trends			**Occupancy linear temporal trends**		
		Estimate	**SDE**	**p-value**	**Estimate**	**SDE**	**p-value**
Species Temperature Index		-0.02765	0.01127	0.01514	0.00030	0.00018	0.10498
Sociality		-	-	0.00469	NA	NA	NA
(ref=Kleptoparasite)	Solitary	0.08152	0.04356	-	NA	NA	NA
	Primitively eusocial	0.24235	0.07334	-	NA	NA	NA
Mean flight date		0.00010	0.00052	0.04588	NA	NA	NA
ITD		NA	NA	NA	0.00086	0.00040	0.03606
Pagel's λ (PGLS)		0; $CI_{95\%}$[0,0.13]			0.08; $CI_{95\%}$[0.01,0.28]		

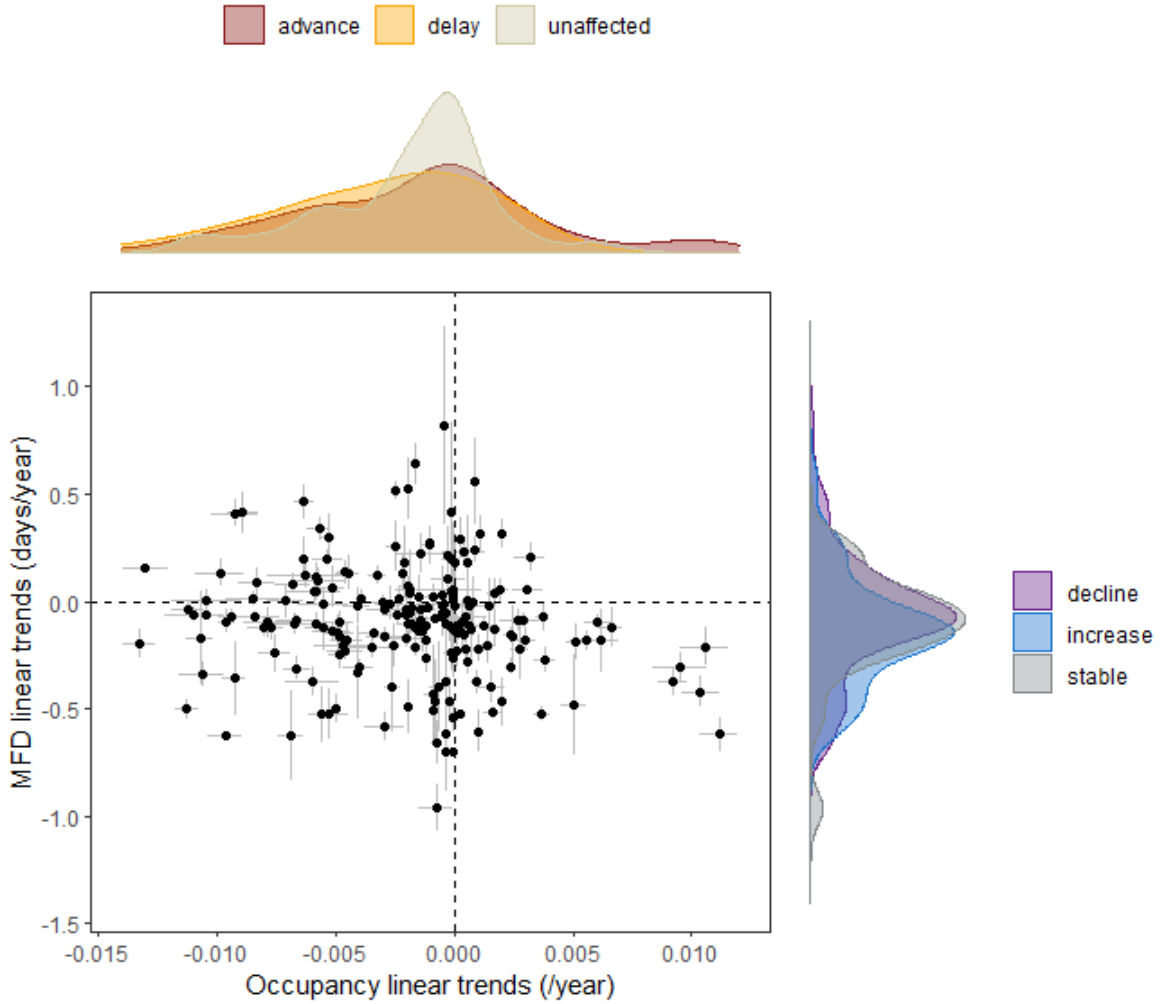
<u>Figure S4:</u> Smoothing of global change drivers. Representation of the smoothing trends in wheat yields and in temperature in function of the smoothing parameter value (*span* parameter of the LOESS).



<u>Figure S5:</u> Robustness analysis to the smoothing parameter values. Sensitivity analysis of the results for occupancy probability changes (a) and mean flight date shifts (b) to the smoothing parameter value (*span* parameter of the LOESS) of wheat yields and temperature as used to construct agricultural intensification and temperature trend drivers respectively. Full circles correspond to effects significantly different from zero, open circles represent effects non-significantly different from zero. Error bars are 95% confidence interval.



<u>Figure S6:</u> Correlation between species temporal trends in occupancy and mean flight date (MFD). Relationship between the linear trends along time of occupancy and mean flight date (MFD), with associated standard errors, and density distributions along axis for crossed species groups. For example, on the right, the blue density distribution represents the distribution of MFD shifts for species having a stable temporal trend in occupancy.



<u>Figure S7:</u> Seasonal variations of the total richness of pollinators over decades and pollination season duration. (a) Pollination season duration, which is the number of days for which the total occupancy of bees is above the given threshold, for 1950 and 2016. (b) Total daily species richness, corresponding to the number of species with a daily occupancy above 0.002, for each decade.

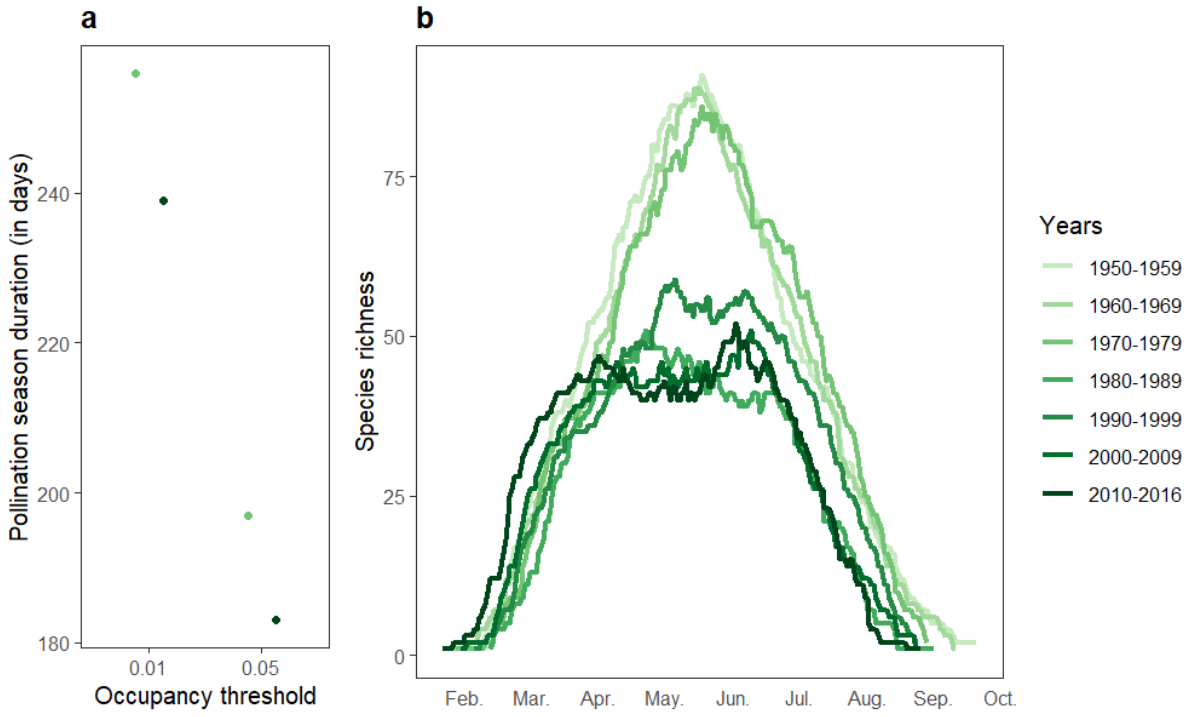


Table S6: Type II ANOVA of the linear-mixed-effect model explaining occupancy yearly changes by global change drivers. AI: agriculture intensification; Urban.: urbanization; ITC: Inter-annual temperature changes; TT: temperature trend.

Variable	Chisq	Df	Pr(>Chisq)
AI	48.1887	1	3.871e-12***
ITC	0.0065	1	0.93579
TT	51.0802	1	8.867e-13***
Urban.	5.8220	1	0.01583
group	45.1857	2	1.542e-10***
AI:group	20.9595	2	2.810e-05***
ITC:group	5.1610	2	0.07574
TT:group	0.1659	2	0.92041
Urban.:group	6.7670	2	0.03393*

Table S7: Type II ANOVA of the linear-mixed-effect model explaining mean flight date yearly changes by global change drivers. AI: agriculture intensification; Urban.: urbanization; ITC: Inter-annual temperature changes; TT: temperature trend.

Variable	Chisq	Df	Pr(>Chisq)
AI	0.0071	1	0.9329
ITC	34.7197	1	3.808e-09 ***
TT	0.0600	1	0.8065
Urban.	0.0101	1	0.9198
group	0.0615	2	0.9697
AI:group	0.0099	2	0.9951
ITC:group	0.8791	2	0.6443
TT:group	0.0715	2	0.9649
Urban.:group	0.0132	2	0.9934

Appendix III

Duchenne F., Martin G. & Porcher E. Not always a debt: northern cost but southern benefit for European plants lagging behind climate. *In review in Ecology Letters*

European plants lagging behind climate change pay a climatic debt in the North, but are favored in the South

Short title: Climatic debts and bonuses in European plants

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Keywords: rang shifts | occupancy trends | climate change | plant distribution | global change drivers

Abstract:

For many species, climate change leads to detectable, but often insufficient, range shifts. Such lag of species range shifts behind climatic conditions is often coined a "climatic debt", but its demographic costs have never been evaluated. Here we jointly assessed temporal shifts in climatic conditions experienced by species and species occupancy trends, for about 4,000 European plant species over the last 65 years. We provide the first piece of evidence that European plants are already paying a climatic debt in Alpine, Atlantic and Boreal regions, but benefit from a surprising "climatic bonus" in the Mediterranean. We also find that among multiple pressures faced by plants, climate change is now on par with other known drivers of occupancy trends, such as eutrophication and urbanization.

Introduction

Climate change is recognized as a major threat for biodiversity (Sala *et al.* 2000). Species have two main ways to persist under such change: they can track their climatic optimum in space (geographic range shift) or they can respond adaptively to survive and reproduce in a modified environment (Chevin *et al.* 2010), i.e. modify their climatic optimum. Concerns about the capacity of species to achieve one or the other quickly enough have increased (Parmesan 2006; Chevin *et al.* 2010; Hoffmann & Sgrò 2011), with many studies showing that living organisms are currently moving poleward and upward in response to climate warming (Parmesan 2006; Kelly & Goulden 2008; Devictor *et al.* 2012; Lenoir *et al.* 2020). Yet, most of those studies so far have shown that range shifts are rarely as fast as climate change (Menéndez *et al.* 2006; Devictor *et al.* 2012; VanDerWal *et al.* 2013; Lenoir *et al.* 2020), i.e. climate variables move faster through space than most species do. This lag of species movements behind climate change is often coined a "climatic debt" (Devictor *et al.* 2012; Monsinjon *et al.* 2019; Lenoir *et al.* 2020). It can be evidenced by a temporal change in the so-called "climatic niche" of a species, as measured by the average of one or several climatic variables throughout its range (VanDerWal *et al.* 2013), hereafter "species climatic indices" (SCI).

Whether the slower movement of species *vs.* climate, or in other words the temporal change in the climatic conditions experienced by a species, indeed represents a "debt" remains to be ascertained. Most species can and do also respond to climate change via adaptive plastic or evolutionary trait changes, which could be sufficient to sustain populations despite changing climatic conditions (Hoffmann & Sgrò 2011), albeit the most recent meta-analysis to date suggests otherwise (Radchuk *et al.* 2019). Thus, to demonstrate the existence of a true climatic debt, one needs to prove that the spatial lag of species *vs.* climate results in decreased individual fitness or decreased population growth, which has never been done so far. Costs associated with the putative climatic debt remain poorly investigated likely because the climatic debt concept has been developed at the community level mostly (Bertrand *et al.* 2011; Devictor *et al.* 2012), while cost estimation is easier at species level, e.g. via an assessment of species persistence. By shifting the concept of climatic debt from community to species level, one can correlate delayed spatial responses (i.e. temporal trends in SCI) with species persistence. Under climate warming, if both species movements and adaptive responses are insufficient, we expect (1) an increase in the species temperature index of a given species over time (limited spatial response) and (2) a negative relationship between the temporal trend in SCI for temperature and the species

persistence (limited adaptive response, Radchuk *et al.* 2019). The latter observation only is suggestive of costs at individual and population levels, i.e. a climatic debt. Alternatively, uncorrelated SCI trends and species persistence would indicate an absence of climatic debt, which could be explained by adaptive responses buffering limited spatial responses or by species insensitivity to temperature (Rodríguez-Sánchez *et al.* 2012). This logic similarly applies to other climatic variables beyond temperature, also a component of climate change. In general, we expect the relationship between SCI trends and species persistence to be weak due to the impacts of numerous other drivers, besides climate change, on the latter. Regardless, under the climatic debt assumption, we expect a significant relationship between SCI trends and species persistence if those additional drivers are taken into account.

Here we examine the temporal shifts in the climatic conditions experienced by a species throughout its range, as measured by SCIs trends, and occupancy trends, a proxy for abundance and future species persistence (He & Gaston 2003), for more than 4,000 European plant species over the last 65 years. These two elements allowed us to verify the existence of a climatic debt, which we estimate via the relationship between occupancy and SCI trends, taking into account other potential drivers of occupancy trends besides climate change via a trait-based approach.

Methods

Data collection and trends in SCI and species occupancy

Plant database

We focused on the most common vascular plant species in geographical Europe, i.e. with at least 500 records in the GBIF database (https://www.gbif.org) between 1950 and 2014 within a rectangle bounded by longitudes [-13°, 34°] and latitudes [34°,75°]. We downloaded all species sightings on the time period from 1951 through 2014, excluding 1950 as this year contains data not precisely dated, but corresponding to the mid-twentieth century. The DOIs associated with the extraction are presented in the Supplementary methods. We considered only records from the European mainland, stopping at 34° of longitude because there were too few data to the East of this meridian (Fig. S1). Note that the area also includes the western part of Turkey. This yielded a dataset containing 111,549,494 occurrence records, characterized by a species name, a location and a date. Of these, we analyzed temporal trends in species climatic indices (SCI) and occupancy only for the species observed at least 20 years between 1951 and 2014 and with at least 1 record between 1951 and 1980. We removed crop species and considered invasive species separately (see Supplementary methods), because the drivers of their occupancy trends are likely quite different from those for native species. This selection

resulted in 4,120 native and naturalized plant species (listed in Table S1), plus 58 invasive species.

Bioclimatic variables

Climate change is not limited to increases in annual mean temperature; hence we characterized the climatic conditions with three bioclimatic variables related to temperature and three bioclimatic variables related to precipitation, because temperature and precipitation are strong predictors of plant distribution (Franklin *et al.* 2013). We used previously published European time series (Fréjaville & Benito Garzón 2018) to extract annual mean temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, precipitation of the wettest month, and precipitation of the driest month. These bioclimatic variables are the same as in Worldclim (bio1, 5, 6, 12, 13, 14) but with annual data. For computational reasons we aggregated 1kmx1km raster cells, which decreased spatial resolution from 1 to about 100km² (~10km×10km).

Calculation of annual species climatic indices and their temporal trends

Species climatic indices (SCI) are often calculated as the average of a climatic variable, e.g. temperature, across a species range (Devictor *et al.* 2012). However, the heterogeneity of opportunistic datasets can seriously skew this index, leading to large biases (Loiselle *et al.* 2008; Beck *et al.* 2014). Because we are not interested in future projections but in inter-annual comparisons we do not need to correct purely spatial biases, but we need to correct temporal biases in the spatial distribution of sampling pressure. The average latitude and longitude of the GBIF records are temporally biased, with a significant decrease with time for both. To reduce such bias we defined annual SCI as the mean climatic variable of all 100km² cells occupied by a given species (≥1 record), while weighting the contribution of each cell by the ratio of the number of records of this species on the number of records of all plant species. Such method enables estimations of the SCI that are more independent from the sampling pressure than a weighting by the number of records of the given species only (Fig. S2).

Based on the method presented above, we calculated one SCI for each bioclimatic variable, species and year. We then assessed the temporal trend in each SCI and species separately, using the following linear model:

$$SCI_k = \mu + \beta \times year_k + \varepsilon_k \quad (1)$$

where SCI_k is the species climatic index of year k, μ is the grand mean (intercept), β is the year effect and ε_k is an error term (independent and identically distributed, following $N(0,\sigma^2)$).

Observations (SCI_k) are weighted by the square root of the number of grid cells included in their calculation for each year.

Occupancy trends

To model the temporal occupancy trends, we first discretized the dataset spatially and temporally, to define areas occupied or not by a species for a given time period. Such discretization allowed us to estimate variation in occupancy probability among time periods by taking the sampling pressure into account (Isaac *et al.* 2014). As for SCI calculation, we used a grid cell of about 10km×10km to discretize the dataset spatially, and we aggregated records temporally by years. For each year, a grid cell is considered as visited by at least an observer if it contains at least one plant species record. The cell is considered as occupied by a species if it contains at least one record of the given species in the given year and unoccupied otherwise. We obtained a dataset composed of annual presences (1) and pseudo-absences (0) in each 10km×10km grid cell.

Before analyzing the data, we discarded all grid cells visited only one year, to improve occupancy estimations by decreasing the confusion between grid cell and year effects (Isaac *et al.* 2014). To save computing time, for each species we removed non-informative grid cells, i.e. cells with no record of the species over the study period. Finally, to estimate a yearly occupancy probability (*p*), we explained remaining presences and pseudo absences for each species separately using the following binomial Generalized Linear Model (GLM) with a logit link:

$$\log\left(\frac{p_{ik}}{1-p_{ik}}\right) = \mu + \beta_1 \times year_k + \beta_2 \times \log(SL_{ik}) + \varphi_i \quad (2)$$

Where p_{ik} is the occupancy probability of grid cell *i* for year *k*, μ is the intercept of the model, β_1 is the year effect (i.e. the occupancy trend), and φ_i a random grid cell effect. Finally, β_2 is the effect of the logarithm of the species list length (SL_{ik}) associated with each grid cell visit (year), which is used as a proxy for the sampling pressure this year. Those models were implemented using the R package *glmmTMB* (Brooks *et al.* 2017). The average occupancy probability for year *k*, p_k, tends to one when all grid cells are occupied and tends to zero when no grid cell is occupied by the given species. We estimated occupancy trends for all native and naturalized 4,120 species, as well as for the 58 invasive species. This latter step allowed us to verify that occupancy trend estimates were large and positive for invasive species (Fig. S3), confirming that the data and statistical methods to estimate occupancy trends yield results consistent with known species trends.

Phylogenetic signal in SCI and occupancy trends

Estimating phylogenetic signal in species response informs us on plausible evolutionary constraints on mechanisms underlying SCI and occupancy trends. To analyze the phylogenetic structure of SCI and occupancy trends, we used the *Daphne* phylogeny of European flora (Durka & Michalski 2012). Of the 4,120 species we analyzed, 1,335 were not included in the phylogeny, thus we excluded them for phylogenetic analysis, and focused on the 2,785 remaining species. We assessed the phylogenetic structure using Pagel's λ, implemented in the *phylosignal* R package (Keck *et al.* 2016), and tested its significance by randomizing the tips of the phylogeny 1,000 times, for both SCI and occupancy trends.

Potential drivers of occupancy trends

The aim of our study was to examine whether occupancy trends can be related to SCI trends; thus, we tried to include other potentially confounding drivers of such trends in the analysis of their relationship. Estimates of temporal occupancy or abundance trends remain scarce in plants, such that their drivers are still largely unknown. Thus, we used the plant and global change literature to identify potential drivers of plant trends, which we took into account via species traits: historical climatic niche (Martin *et al.* 2019), lifespan (Martin *et al.* 2019), habitats affinity (Aronson *et al.* 2014; Buse *et al.* 2015), nitrophily (Sala *et al.* 2000; Bobbink *et al.* 2016), moisture preferences (Moeslund *et al.* 2013) and pollinator dependency (Biesmeijer *et al.* 2006). We detail all calculations for these traits in Supplementary Methods.

Species traits, SCI and occupancy trends are available in Table S1.

Evidencing the climatic debt: relationship between SCI trends and occupancy trends

Analysis at continental scale

As explained above, a climatic debt can be revealed by a negative relationship between species occupancy trends and SCI trends. To assess this relationship between SCI trends and occupancy trends, taking into account the species traits cited above, we used linear models. We first checked the correlations among the six SCI trends and six historical climatic niche indices. We noticed high correlations (r>0.7) among historical temperature indices, among historical precipitation indices, among SCI trends related to temperature and among SCI trends related to precipitation (Fig. S4). In order to avoid multicollinearity issues, we selected two indices for the historical climatic niche (annual mean temperature and precipitation) and three SCI trends: annual mean temperature, annual precipitation, and precipitation of the driest month. We selected annual indices for historical climatic niche and SCI trends as they are the most used

and integrative bioclimatic variables, and we added SCI trends of precipitation of the driest month because the latter was not highly correlated with annual precipitation (Fig. S4).

In summary, we considered the following correlates of occupancy trends: SCI trends related to annual mean temperature, annual precipitation and precipitation of the driest month, historical climatic index related to annual mean temperature and annual precipitation, nitrophily and moisture EIV, pollinator dependency, habitat affinity and lifespan. To be able to compare the strength of relations across explanatory variables, we scaled them before using the Phylogenetic Generalized Least Squares (PGLS) regression, except for habitat affinity and lifespan, as we wanted to extract the effect on the intercept for the first and as the second is a qualitative variable. We used the PGLS function implemented in the *caper* R package (Orme *et al.* 2013):

$$\Delta O_{kj} = \mu + \beta_1 \times \Delta SCI_{bio1_k} + \beta_2 \times \Delta SCI_{bio12_k} + \beta_3 \times \Delta SCI_{bio14_k} + \beta_4 \times BCI_{bio1_k} + \beta_5 \times BCI_{bio12_k} + \beta_6 \times ME_k + \beta_7 \times NE_k + \beta_8 \times Poll_k + \theta_j + \sum_{i=1}^{h} \beta_{habitat_i} \times Habitat_i + \varepsilon_{kj} \quad (4)$$

Where ΔO_{kj} is the occupancy trend of species *k* with lifespan class *j*, μ is the grand mean (intercept), $\beta_1$and β_2 are the slopes of SCI trends, β_4 and β_5 are the effects of historical climatic niche indices, BCI_{bio1} and BCI_{bio12}, related to annual mean temperature and annual precipitations respectively. β_6 and β_7 are the effects of Ellenberg index values for moisture and nitrogen respectively. β_8 is the effect of pollinator dependency, θ_j is the qualitative lifespan effect and $\beta_{habitat_i}$ is the effect of affinity to habitat *i*, with six habitat classes (*h* = 6, Table S2), woodland being the reference habitat. ε_k is an error term, independent and identically distributed, following $N(0,\sigma^2)$, after correction by Pagel's λ value at the likelihood maximum.

This model included all species comprised in the phylogeny and for which there was no missing trait (*n* = 2,013). To include the 67 species that were not in the phylogeny but for which all traits were available, we also performed a linear mixed-effect model similar to the PGLS but including random taxonomic effects of the class (φ_c) and of the family (φ_f) instead of a phylogeny:

$$\Delta O_{kjcf} = \mu + \beta_1 \times \Delta SCI_{bio1_k} + \beta_2 \times \Delta SCI_{bio12_k} + \beta_3 \times \Delta SCI_{bio14_k} + \beta_4 \times bio1_k + \beta_5 \times bio12_k + \beta_6 \times ME_k + \beta_7 \times NE_k + \beta_8 \times Poll_k + \theta_j +$$

$$\sum_{i=1}^{h} \beta_{habitat_i} \times Habitat_i + \varphi_c + \varphi_f + \varepsilon_{kjcf} \quad (5)$$

This linear mixed-effect model was weighted by the inverse of the standard errors associated with the occupancy trends (from equation 3).

Analysis by biogeographic region and time period

In order to examine the spatial variation in climatic debt, we also conducted the same analysis within biogeographic regions. We focused on the five biogeographic regions with at least 1,000 species: Alpine, Atlantic, Boreal, Continental and Mediterranean regions. For each region, as for the main analysis, we retained only species with at least 20 years of data.

We re-calculated SCI and occupancy trends within each region independently, using the same method as described above, but including only plant records from the focal biogeographic region. With these new estimates, we assessed regional climatic debts as the relationship between SCI and occupancy trends, using the same models as in the European analysis (equations (4) and (5)). While SCI and occupancy trends were calculated within biogeographic regions, we considered other species traits as constant throughout Europe and kept the same values across regions.

Finally, to confirm that the costs of the shifts in experienced climatic conditions occur only after the acceleration of climate change (1980-2000, Fig. S5) we performed the same set of analyses on the earliest data, taking the first 40 years (1951-1990) to retain enough records and years to estimate SCI and occupancy trends. We calculated SCI trends and occupancy trends between 1951 and 1990. For SCI trends, we used only records from 1951 to 1990. For occupancy trends, we used all records and the same model as in equation (2) but with a broken-line model for the year effect, as implemented in the *segmented* R package (Muggeo 2008), with a breakpoint in 1990. Such method enables estimation of random site effects and effect of the species list length on the entire dataset while modelling a trend for 1951-1990. Results are shown in Fig. S6.

Combining the effects of precipitation and temperature SCI trends to estimate an overall climatic debt

To combine the effects of annual precipitation and temperature SCI trends on occupancy trends for each biogeographic region, we multiplied each unscaled effect of SCI trends by the observed change in the corresponding climatic indices. This yielded a measure of the effective cost/bonus due to a given SCI trend, i.e. to the lag of species behind climate change. For each region, we then summed the values of effective cost/bonus for temperature and precipitation to

get a measure of the overall climatic debt/bonus over the study period. We also calculated the relative contribution of precipitation and temperature SCI trends to the overall debt/bonus by dividing each by the sum of the absolute values of both.

Results

Temporal trends in Species Climatic Indices

During the study period (1951-2014), all SCIs change significantly, in direct relation with climate change. All bioclimatic variables related to temperature and precipitation increase on average over the study area, but with substantial spatial heterogeneity for precipitation (Fig. S5). Consistently with the trends in bioclimatic variables related to temperature, we show that the temperature SCIs increase over time for a large majority of species (Fig. 1). Precipitation SCIs also increase over time on average (Fig. 1), but the distribution of precipitation SCI is closer to zero, with more numerous negative trends than for temperature SCIs.

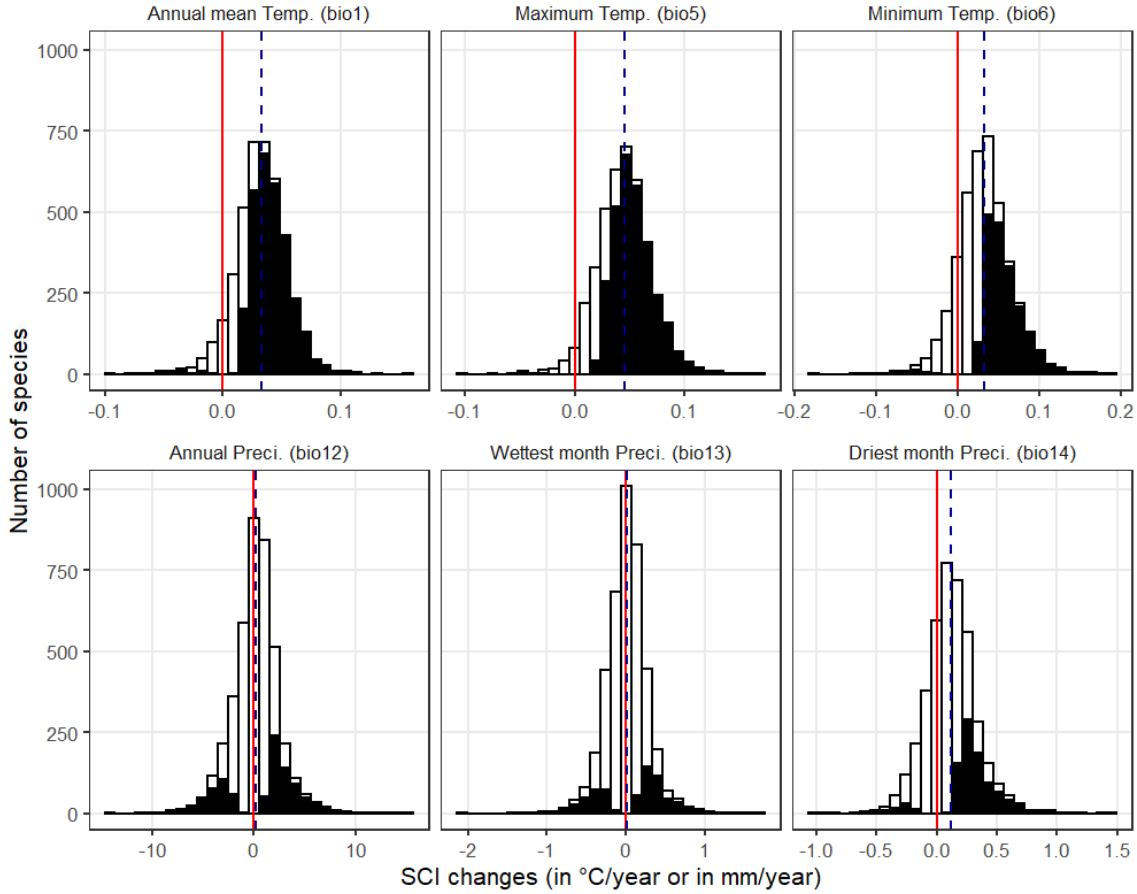

***Figure 1:* Linear trends in species climatic indices (SCI) for all species (n=4,120).** *The first row shows the trends in temperature SCIs and the second row the trends in precipitation SCIs over time. The vertical red line indicates zero (no change across years) while the vertical dashed blue lines show the average values across the 4,120 species. Filled bars represent the count of species with significant trends (p-value<0.05) whereas open bars represent the count of species with non-significant trend (p-value>0.05).*

We find a significant phylogenetic signal in all SCI trends (Fig. 2), but trends in temperature and precipitation SCIs are not significantly correlated (Fig. S4), probably due to the fact that annual precipitation and temperature trends exhibit contrasting spatial distributions (Fig. S5c-d).

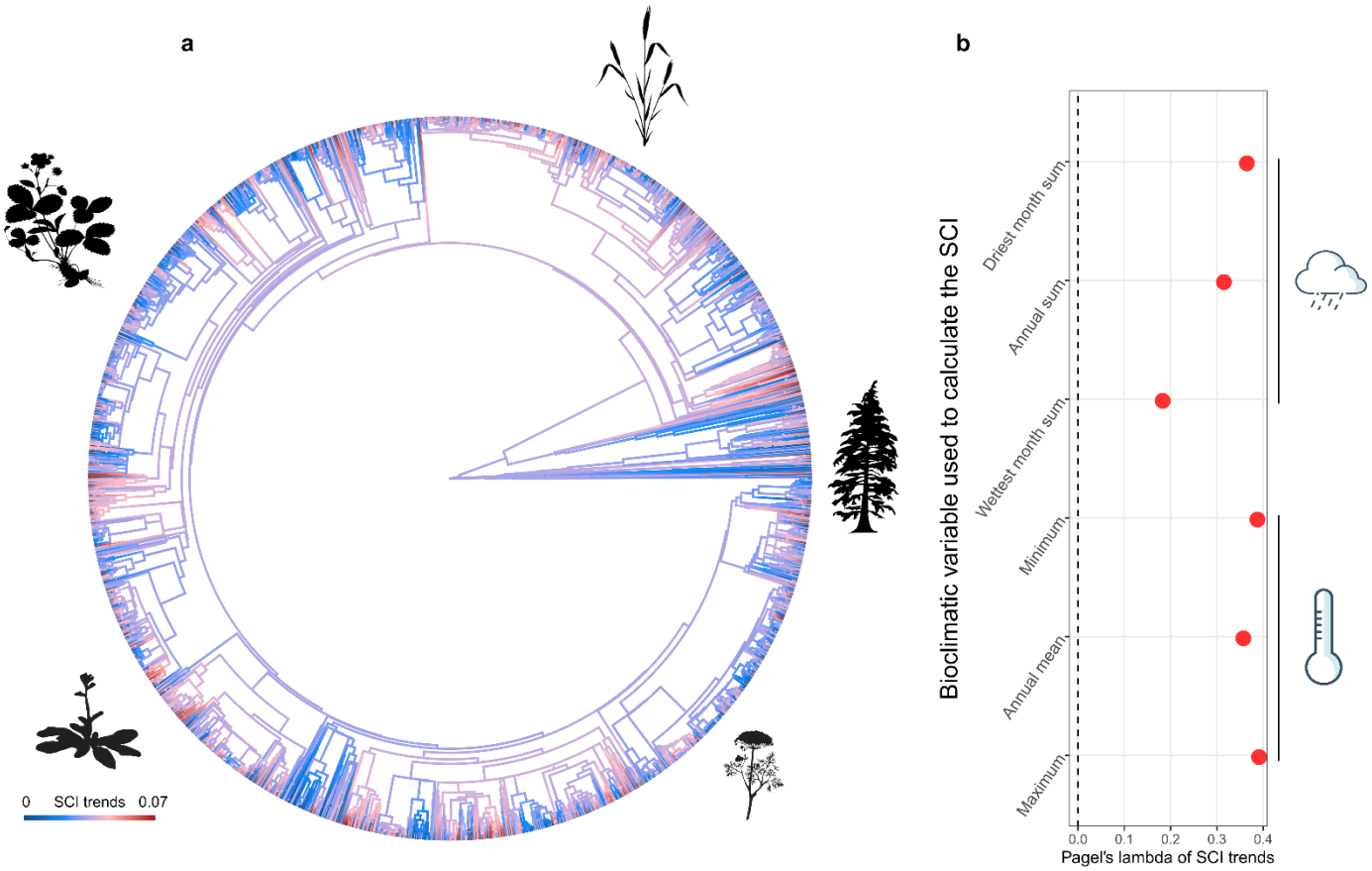

Figure 2: ***Phylogenetic signal in the linear trends in species climatic indices (SCI) for 2,785 species included in the phylogeny****. (a) Phylogenetic signal in the SCI trends related to the annual mean temperature bioclimatic variable (bio1). The color scale is bounded between the 5th and 95th quantile to preserve readability. (b) Pagel's λ for SCI trends related to the six bioclimatic variables. Zero (dashed black line) indicates an absence of phylogenetic signal. Red circles correspond to a significant phylogenetic signal (p-value < 0.05, calculated from 1000 randomizations).*

Occupancy trends and their drivers

The average trend in occupancy over all native and naturalized species is slightly positive: $0.0048 \pm 3.29\ 10^{-4}$ year^{-1} (mean ± SE), but the number species with significant increase in the occupancy estimates (1,721 species, 42%) is comparable to the number of species with significant decline in occupancy (1,519 species, 37%). The average positive trend over all species (Fig. 3a) is mainly explained by the skewed distribution of trends towards positive values, with a couple of species exhibiting strong increases even after exclusion of invasive species (Fig. S3). Furthermore, we find that plant occupancy trends exhibit a strong

phylogenetic signal both before (Pagel's λ = 0.62, p-value<0.01; *n*=2,785) and after (Pagel's λ = 0.45, $CI_{95\%}$ = [0.32,0.57]; *n*=2,013) taking into account species traits.

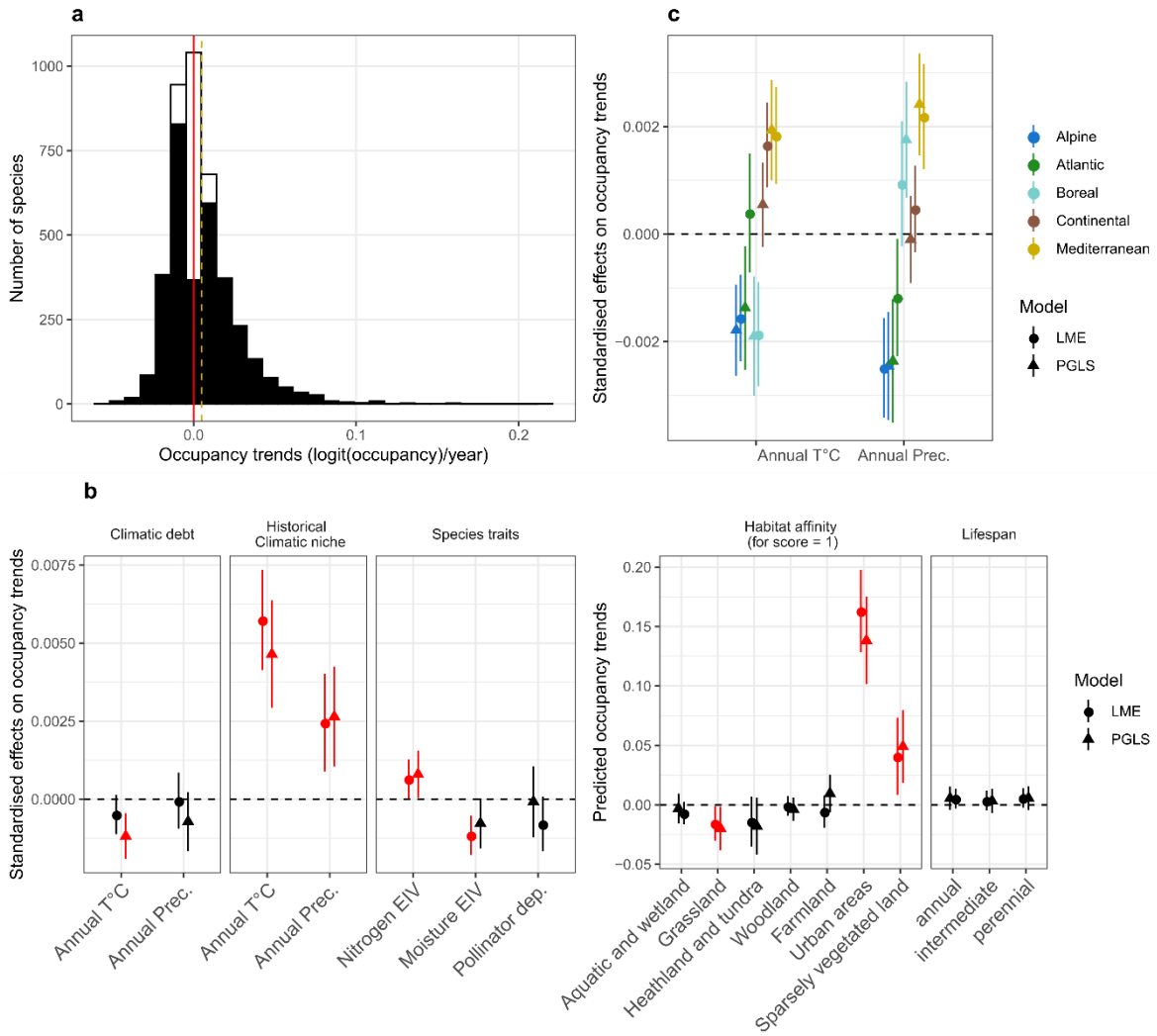

***Figure 3:* Occupancy trends and their correlates.** *(a) Histogram of occupancy trends, on a logit scale y^{-1}. The red vertical line indicates zero while the vertical dashed blue line shows the average value (n=4,120). Filled bars represent the count of species with significant trends (p-value<0.05) whereas open bars represent the count of species with non-significant trends (p-value>0.05). (b) The left panels represent the estimates (±$CI_{95\%}$) from phylogenetic regressions (PGLS, n=2,013) and linear mixed-effect model (LME, n= 2,080, see Methods) explaining occupancy trends with temporal trends in SCI and other species traits. The right panels show predicted averaged occupancy trends (±$CI_{95\%}$) for annual species with complete affinity for each habitat (habitat affinity score = 1 and lifespan = annual), and for lifespan categories, predicted at the average of all other variables. Red symbols represent significant effects while black symbols represent non-significant correlations. (c) Estimates (±$CI_{95\%}$) from PGLS and LME of the effect of standardized temperature and precipitation SCI trends on occupancy trends, for each biogeographic region.*

The analysis of the correlates of species occupancy trends reveals that plant species pay a climatic debt, but only in some parts of Europe. While at the continental scale, the negative relationship between SCI trends and occupancy trends is not significant (Fig. 3b), analysis by

biogeographic regions reveal significantly correlations, with a strong heterogeneity among regions and across bioclimatic variables. Regarding temperature, in the two coldest biogeographic regions (i.e. Boreal and Alpine regions), a temporal increase in temperature throughout a species range, a consequence of an insufficient range shift to keep pace with historical climatic conditions, is associated with lower occupancy probabilities over time (Fig. 3c). Surprisingly, in the warmest Mediterranean region, the opposite pattern is observed, i.e. species that have experienced a temperature increase throughout their range tend to increase (Fig. 3c), suggesting that climate change elicits a bonus instead of a debt in this area. Regarding precipitation, plant species occupancy trends are negatively related with precipitation SCI trends in the Alpine and Atlantic regions with the highest rainfall, while this relationship tends to be positive in the drier Boreal, Mediterranean and Continental regions (Fig. 3c).

These contrasting consequences of lagging behind climate change come in addition to expected effects of the historical climatic niche (Fig. 3b), that however vary in space. At the continental scale, species from rainy and warm historical niches exhibit higher occupancy trends. However, within biogeographic regions, the advantage of warm historical niches was true only in cooler parts of Europe (Boreal, Atlantic and Alpine regions, Fig. S7). Similarly, the benefit of rainy niches is seen in Boreal and Continental regions only (Fig. S7), where rainfall has increased the most (Fig. S5), while species with dry niches seem to be favored in the Alpine region with decreasing precipitation (Fig. S7).

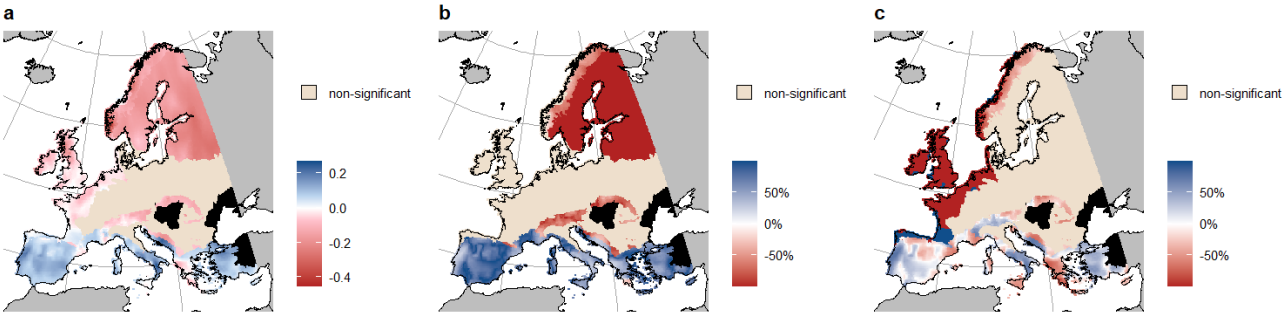

Figure 4: ***Climatic debt/bonus in Europe and its climatic drivers.*** *(a) Climatic debt/bonus averaged over all species over the last 65 years. The gradient from white to red indicates a climatic debt (cost of climate change in terms of species occupancy), while the gradient from white to blue indicates a climatic bonus (benefits of climate change in terms of species occupancy); white represents no cost of range shift lags on average for plants. Relative contribution of (b) temperature and (c) precipitation SCI trends to the climatic debt/bonus, in percentage. Black regions are biogeographic regions with too few data. The maps were generated using only predicts for effects of SCI trends that are significant in both the phylogenetic regression and the linear mixed-effect model averaged over both models, LME and PGLS.*

The overall consequences of climate change, combining both temperature and precipitation variables, are a climatic debt in Alpine, Atlantic and Boreal regions (Fig. 4a), but a climatic bonus in the Mediterranean (Fig. 4a), driven mostly by temperature changes but with a significant contribution of precipitation locally (Fig. 4b,c). In the Continental region the observed lags in range shifts did not have any overall significant effect on plant persistence (Fig. 4a), although when combining all the non-significant effects, lags in range shifts tended to benefit plants there, similarly to the Mediterranean region (Fig. S8). The examination of the relative contributions of temperature and precipitation SCI trends to the climatic debt/bonus shows that temperature is generally the major driver (Fig 4c), except in the Atlantic region, where precipitation shifts are the only significant driver of estimated climatic costs.

Finally, plant species occupancy trends are also expectedly related to other drivers beyond climate change. At a continental scale, nitrophily and urban affinity are significant correlates of plant occupancy trends (Fig. 3b). We also find a negative but non-significant effect of pollinator dependency on occupancy trends (Fig. 3b). A majority of the remaining variables, such as most habitat affinities except urban affinity and moisture preferences, have contrasting effects on occupancy trends across biogeographic regions (Fig. S7).

Discussion

Our study of the consequences of climate change for plant species first confirms a spatial lag in species responses to climate change, evidenced by an increase in both temperature and precipitation SCIs (Fig.1) suggesting that species are not moving fast enough to track their historical climatic conditions (i.e. to keep constant SCIs). Those SCI trends are phylogenetically structured, which could be explained by the already known climatic niche conservatism in plants (Prinzing Andreas *et al.* 2001; Preston & Sandve 2013; Hawkins *et al.* 2014; Liu *et al.* 2015) but also by the phylogenetic structure in the ability of plant species to track their optimum spatially via colonization (Baeten *et al.* 2015). Furthermore, we also find that temperature and precipitations exhibit very different temporal trends in Europe, inducing SCI changes that are not correlated, possibly leading to a trade-off between tracking precipitation and temperature historical conditions spatially for European plants, as has been shown along the elevation gradient (Crimmins *et al.* 2011).

Analyses within biogeographic regions reveal that the lag in species response to temperature change translated into a climatic debt in the North but a surprising climatic “bonus” in the South, resulting in no overall signal for a climatic debt at the European scale. In Boreal and

Alpine regions, the effect of temperature SCI trends comes in addition to an effect of the baseline climatic niche, with larger occupancy trends for species from warmer area historically. This pattern is consistent with previous results on French plants (Martin *et al.* 2019), and its significance only in the cooler parts of Europe (Fig. S7) confirms the well-known stronger effect of climate warming at higher latitudes (Parmesan 2007). That occupancy trends correlates significantly both with temperature SCI trends and temperature of the historical niche in cooler parts of Europe suggests that climate is an important driver of species persistence in these areas. In contrast, the surprising climatic bonus in the Mediterranean region is consistent with the absence of correlation between the baseline climatic niche and occupancy trends there, suggesting that climate is currently not a strong driver of plant occupancy trends in this area, as previously shown for colonization patterns (Normand *et al.* 2011). This unexpected climatic bonus, which is generally overlooked, could be caused by changes in competitive interactions, an important driver of species responses to climate change (Alexander *et al.* 2015). Plants with limited or no northward shift (i.e. plants with an increasing temperature SCI) may benefit from competitive release associated with the range shift of more mobile species, without being in competition with novel competitors from southern regions, because of the numerous geographic barriers limiting plant colonization in the Mediterranean region (Normand *et al.* 2011). Such result suggests for the first time that a lag in species range shift can sometimes benefit plant species, at least over a few decades. These benefits are however likely to be reversed by sustained climate change on the longer term when climatic conditions exceed the climatic tolerance of species.

In addition to these effects of temperature, the climatic debt can also be driven by changes in precipitation, albeit to a lesser extent. When we combine the effects of temperature and precipitation SCI trends, we show that the inability of plant species to track their historical climatic conditions has been costly in the Alpine, Atlantic and Boreal regions, but beneficial in the Mediterranean region. These patterns substantiate further the notion of climatic debt in the former areas, and confirm the climatic bonus in the Mediterranean, although lags behind climate are most often interpreted as a climatic debt there (Bertrand *et al.* 2016). The effects of lagging behind changing precipitations are variable however. In relatively dry biogeographic regions, a decrease in the annual precipitation SCI of plant species over the past decades is associated with negative, or less positive, occupancy trends, which suggests that climate change causes water-deficit stress with detrimental consequences for plant population dynamics, a well-known phenomenon (Breshears *et al.* 2005; Allen *et al.* 2010; Zhao & Running 2010). This applies to

the Mediterranean region, in which precipitation shifts can be as important a driver as temperature changes, although it is widely overlooked in climatic debt assessments. In contrast, in relatively wet areas, plant occupancy trends seem to be hindered by an increase in annual precipitation SCI, which suggests water-excess stress, via e.g. waterlogging. Such consequences of climate change, via an increase in precipitation, is less documented but has been shown to drive downhill shifts in plant species elevation against temperature changes in mountain areas (Crimmins *et al.* 2011). Their general contribution to the climatic debt relative to temperature is however moderate, except in the Atlantic region.

Beyond the effects of climate change, our results also confirm the role of nitrogen deposition and urbanization as important biodiversity disturbance (Aronson *et al.* 2014; Bobbink *et al.* 2016). However, while nitrogen deposition is sometimes cited as the first driver of changes in plant species composition (Bobbink *et al.* 2016), our results challenge this statement: by assessing response traits simultaneously, we find stronger links of occupancy trends with historical climatic niche or urban affinity than with nitrophily. Hence, our results are consistent with the recent acceleration of climate change in Europe and suggest that climate warming has caught up with urbanization and nitrogen deposition to become an important driver of plant persistence. We thus provide further evidence that biodiversity is often affected by multiple global change drivers rather than by single threats (Brooks *et al.* 2017). Consistently with previous results and with the pollinator decline (Biesmeijer *et al.* 2006), we find a negative effect of pollinator dependency on occupancy trends, but the latter is non-significant. This lack of signal for an effect of pollinator loss on plant occupancy trends may be attributable to contrasting plant trends depending on the group of pollinators (Biesmeijer *et al.* 2006).

Here we show that plants are under multiple pressures from global change, and that plant occupancy trends exhibit a strong phylogenetic signal, which entails a risk of important evolutionary history losses associated with the forecasted extinctions. In particular, in some regions plant persistence is already affected by climate change and the resulting climatic debt/bonus, while these climate-related costs/benefits are often considered long-term. The climatic debt/bonus that we evidence here is an integrative measure of all ecological and evolutionary costs/benefits associated with climate change, which we are not able to partition. For example, the costs we observe in Northern Europe could be due to insufficient adaptive response to buffer a spatial lag, to the arrival of novel competitors (Alexander *et al.* 2015), and/or to the demographic cost of an ongoing adaptive response (Lynch & Lande 1993) buffering the spatial lag. As plant adaptation to climate change opens the door to a possible

evolutionary rescue for species that track their climatic optimum poorly in space (Gonzalez *et al.* 2013), assessing the contribution of ecological and evolutionary mechanisms of the climatic debt or bonus is a remaining key challenge to predict future effects of climate change on plants.

Finally, we present the first overview of plant occupancy trends at continental scale. This was made possible by the use of opportunistic data, which are often the only data source to obtain long time-series at large spatial extent (Biesmeijer *et al.* 2006; Bartomeus *et al.* 2019), together with statistical methods thought to correct the potential biases associated with those data (Isaac *et al.* 2014). The fact that we find strong positive trends for invasive species confirm that trends estimated from GBIF data provide an accurate picture of actual changes in species occupancy. However, finding independent datasets and methods that allow to turn the clock back and study past effects of global change on biodiversity is a major challenge to confirm such results and anticipate future threats for biodiversity.

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Author Contributions

FD designed the study, extracted the data and performed all the statistical analyses. GM and FD extracted and compiled species traits. FD and EP wrote the paper with contributions from GM.

Competing interests

The authors declare no competing interests.

Data availability statement

All data and scripts will be publicly available upon manuscript acceptance.

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Supplementary Methods:

DOIs

For computational reasons we split the extractions from the GBIF into 10 parts, accessible through the 10 followings DOI:

- GBIF.org (01 May 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.z8kcad
- GBIF.org (01 May 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.fyakne
- GBIF.org (01 May 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.7u7dgx
- GBIF.org (01 May 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.ske4qr
- GBIF.org (01 May 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.bhfw37
- GBIF.org (01 May 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.zy2nhr
- GBIF.org (01 May 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.67dgze
- GBIF.org (30 April 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.3b8bc8
- GBIF.org (30 April 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.p5awfb
- GBIF.org (30 April 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.kjv523

Plant species selection

We removed crop and ornamental species from this list, using an FAO reference list for crop species (http://www.fao.org/fileadmin/templates/ess/documents/world_census_of_agriculture/appendix4_r7.pdf) complemented by visual inspection of the list. We also considered invasive species separately; they were identified using the European Union list for invasive species (https://ec.europa.eu/environment/nature/invasivealien/index_en.htm), complemented by visual inspection. By definition, invasive species have increased in abundance/occupancy in the recent past; this allowed us to check that occupancy trends as calculated below were able to detect these increases (Fig. S4).

Potential drivers of occupancy trends

For each species, we calculated historical climatic indices for the six bioclimatic variables studied here. To do so, we averaged SCIs over 1951-1980 (i.e. stopping before the recent sharp temperature increase, Fig. S2a) for each species, weighting each year by the number of records of the given species.

For nutrient (reflecting mainly nitrophily) and moisture preferences we used the Ellenberg Indicator Values (EIV) from France (Julve 1998), United-Kingdom (Fitter & Peat 1994), Italy (Pignatti *et al.* 2005), Czech Republic (Chytrý *et al.* 2018) and Germany (Ellenberg *et al.* 1992). All EIVs are on the same scale, but they are a relative measure of species preference, depending on the species assemblages used. As these species assemblages depend on the source, a given

value can reflect distinct nutrient/moisture preferences among sources. Using species shared across EIV sources, we corrected biases among data sources, using the following formula:

$$EIV_{x_s}{}' = EIV_{x_s} + \frac{\sum_{j=1}^{n} EIV_{Baseflor_j} - EIV_{x_j}}{n} \quad (3)$$

where EIV_{x_s} is the Ellenberg indicator value of species *s* in source *x* and *n* the number of species shared between the source *x* and Baseflor, which was used as a reference because it contains information for the largest number of species. Finally, for species present in several data sources we used the average corrected EIVs, over all sources. The whole procedure was performed independently for moisture and nutrient preferences.

Pollen vector (i.e. insects, wind or self-fertilization) was retrieved from the Baseflor (Julve 1998), Ecoflora (Fitter & Peat 1994) and BiolFlor (Kühn *et al.* 2004) databases. Many species are associated with several types of pollen vectors, both within and among databases. We encapsulated this variability into a single variable: pollinator dependency, the percentage of times "insects" appear as a pollen vector for a given species, across all databases. Pollinator dependency ranges from 0, for species that are never associated with insect pollination in the trait databases and that should be therefore independent of pollinators for their reproduction, to 100, for species that are only associated with insect pollination, and that should be strictly dependent on pollinators for their reproduction.

The lifespan of each species was extracted using the R package *TR8* (Gionata 2015) and coded following Martin et al.'s (2019) categories but with three levels only: strict annual plants, intermediate plants (biennial, annual/perennial, etc.) and strict perennial plants.

Habitat affinity was calculated following the same principles as for SCIs, but averaged over the whole time period (1951-2014). We used the EUNIS habitat classification (Davies *et al.* 2004) at the first level, but merging all aquatic, wetland and coastal habitats together (Extended Data Table 1). For each 10km×10km grid cell, we calculated the percentage of area covered by each habitat. Then, for each species and each habitat, we calculated the weighted mean of the habitat coverage over the range of each plant species, weighting the contribution of each cell (10×10km²) by the ratio of the number of records of this species on the number for records for all plant species. For each species, we therefore obtained 7 habitat affinity indices, each ranging from 0 to 1 and summing to 1 across habitats. They correspond to the fraction of a given habitat in the species distribution.

Species traits, SCI and occupancy trends are available in Supplementary Table 1.

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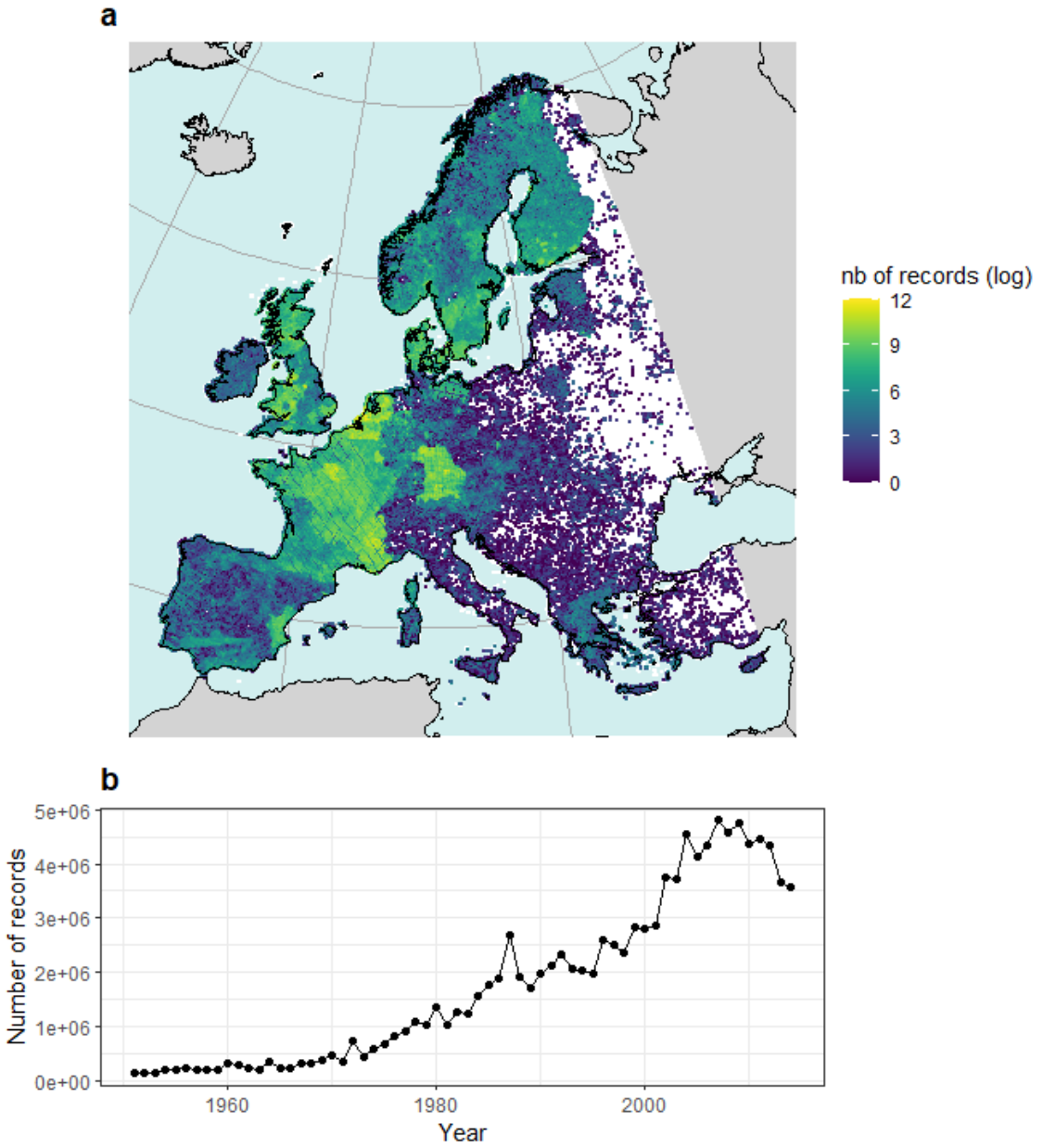


Figure S1: ***Spatial and temporal distribution of the records used.*** *(a) Spatial distribution of the records used, grouped by ~100km² grid cells. White grid cells correspond to cells with no data and grey cells are outside of the study area. (b) Number of annual records through time, showing a continuous geometric increase over years in the number of data.*

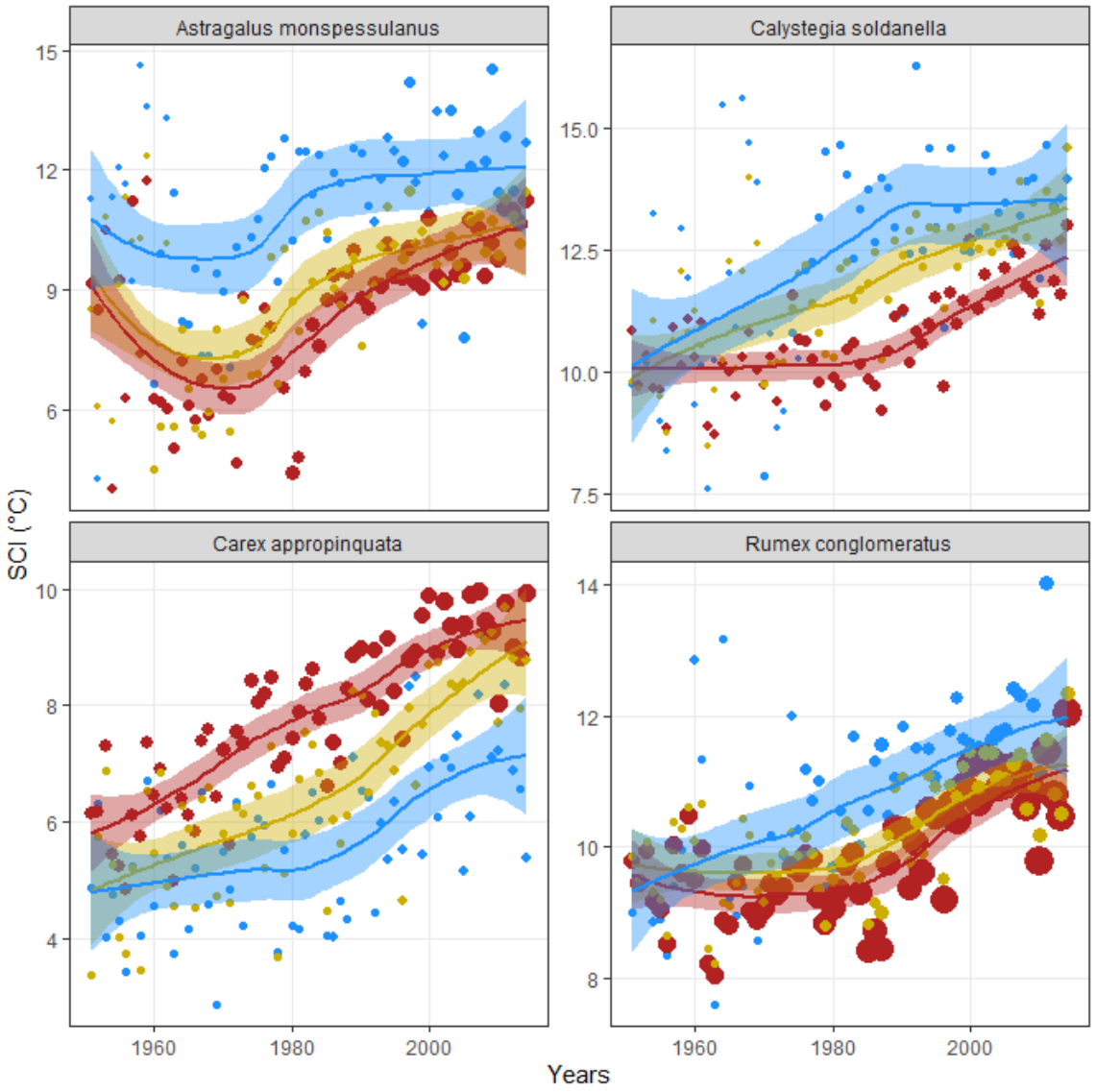


Figure S2: *Examples of interannual variability in SCI, using annual mean temperature. SCI when calculated by taking sampling pressure into account (blue) or when sampling pressure is neglected (yellow). The red curve and circles represent the temperature index calculated from the sampling pressure, on the distribution area of the focal species (all grid cells with at least one record of this species on 1951-2014). These values were calculated as the blue one (see Methods) but by weighting the temperature mean by the number of records of all species studied (instead of the number of records of the focal species) divided by the number of records of all species studied. Thus, the red curve shows temporal bias in the sampling pressure in addition to real variations of temperature. Circle size is proportional to the number of grid cells included in the (weighted) mean. Curves are the results of LOESS regressions implemented in ggplot2.*

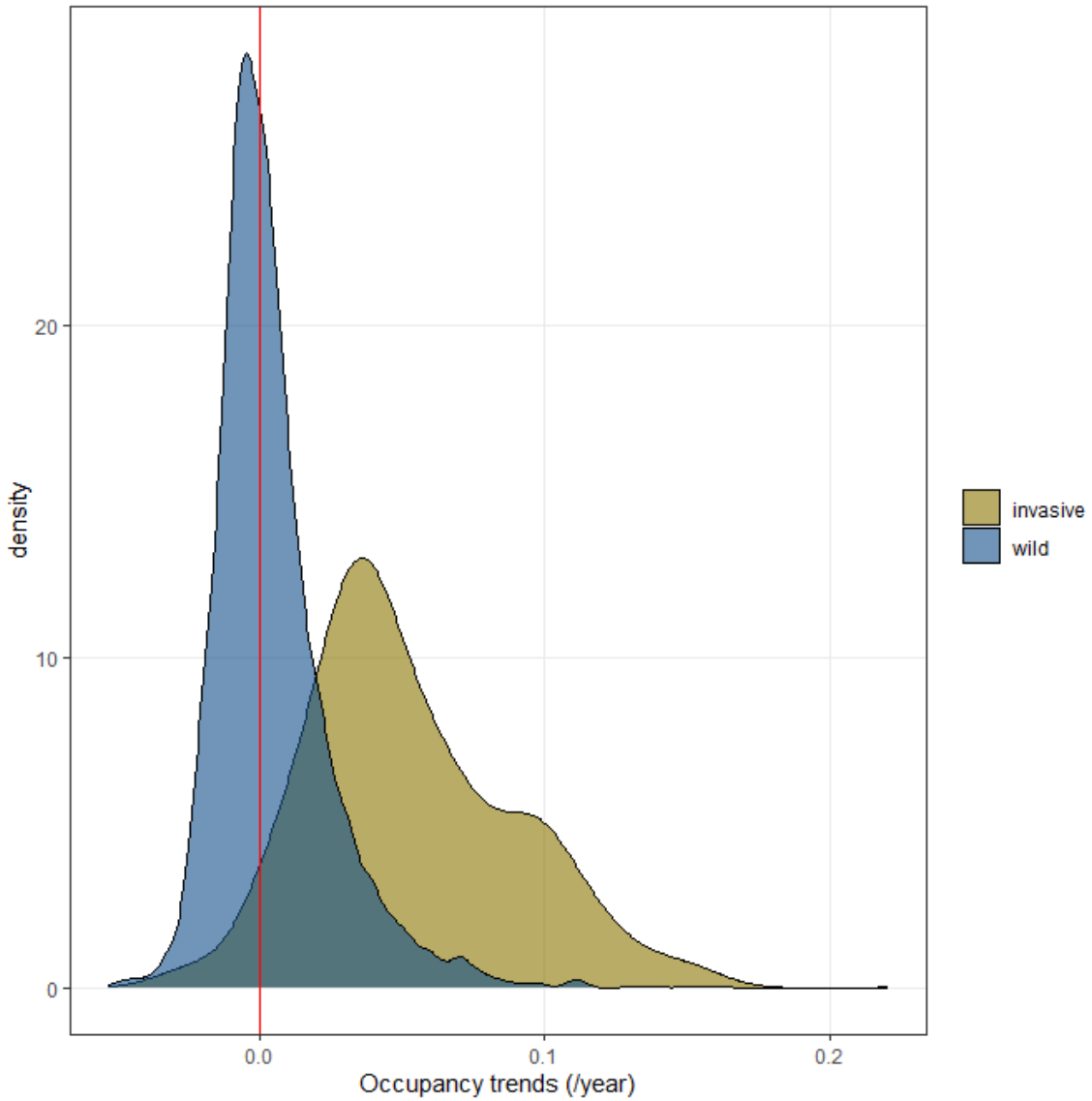


Figure S3: ***Occupancy trends of native or naturalized vs. invasive species****. Density distribution of occupancy trends for the 4,120 native or naturalized ("wild") species and for the 58 species that were identified as "invasive" in the species selection. The red vertical line indicates zero.*

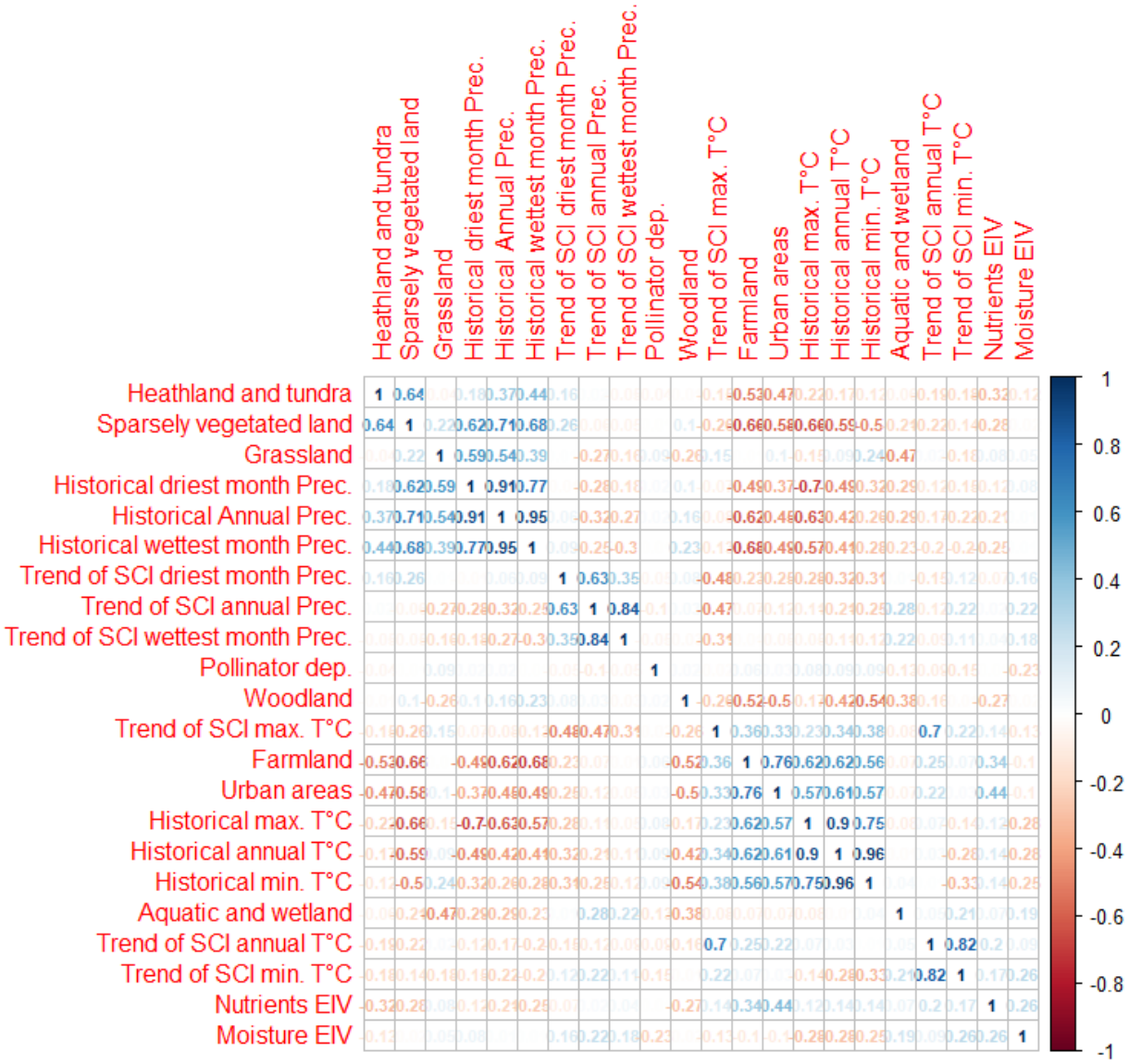


Figure S4: ***Correlation matrix among variables potentially added to PGLS and LME.*** *The red to blue color ramp represents the sign and strength of the correlation. Variables are ordered in the matrix so that highly correlated variables are clustered.*

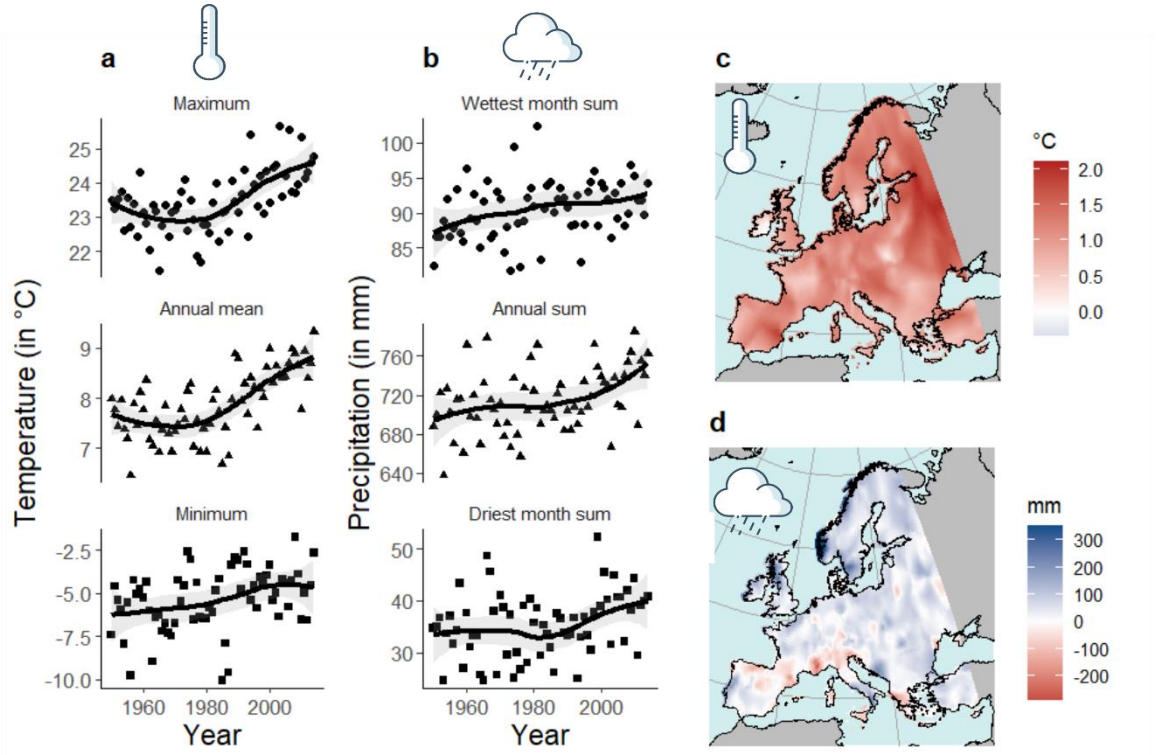


Figure S5: ***Change in bioclimatic variables across time and space****. (a) and (b) show temporal variations in temperature and precipitation respectively, averaged over the study area. Circles depict maximum temperature or precipitation of the wettest month (bio5 & 13), triangles annual mean temperature or annual precipitation (bio1 & 12), and squares minimum temperature or precipitation of the driest month (bio6 & 14). The black lines correspond to LOESS (Locally Estimated Scatterplot Smoothing) curves obtained from the ggplot2 library in R. (c) and (d) illustrate the spatial variation in temporal changes of annual mean temperature and precipitation respectively. Temporal changes were measured here as the difference between the 1950-1960 average and the 2004-2014 average. In (d) the upper bound of the color scale is truncated to 350mm instead of 575mm to preserve readability.*

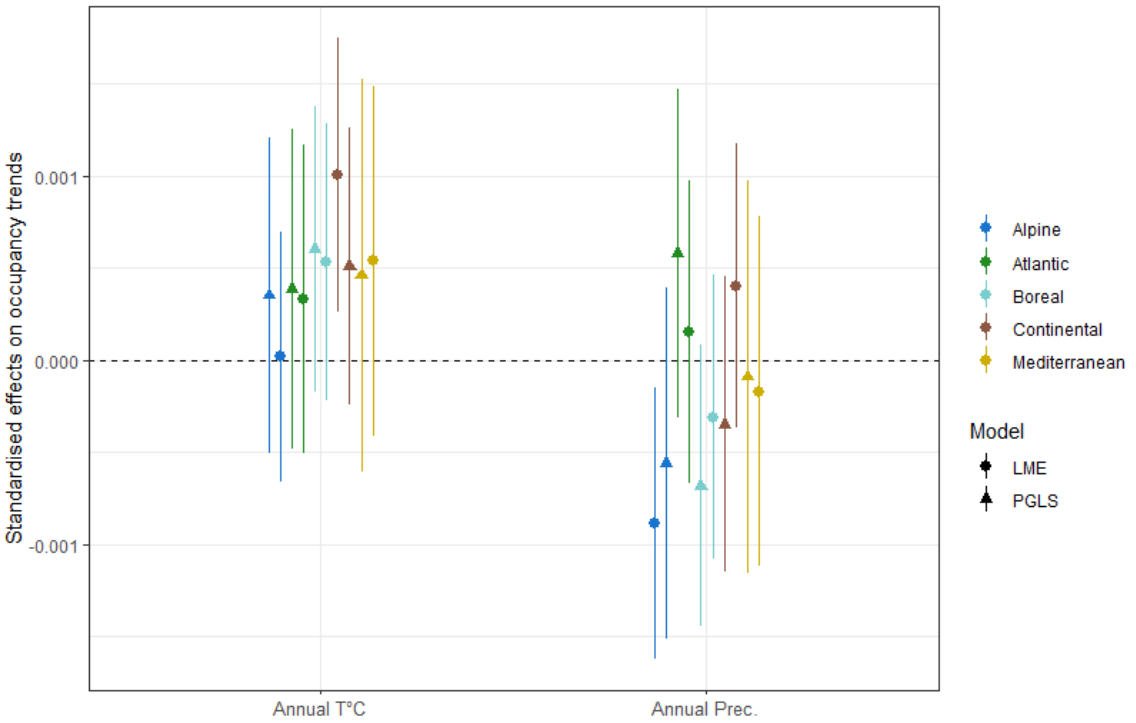
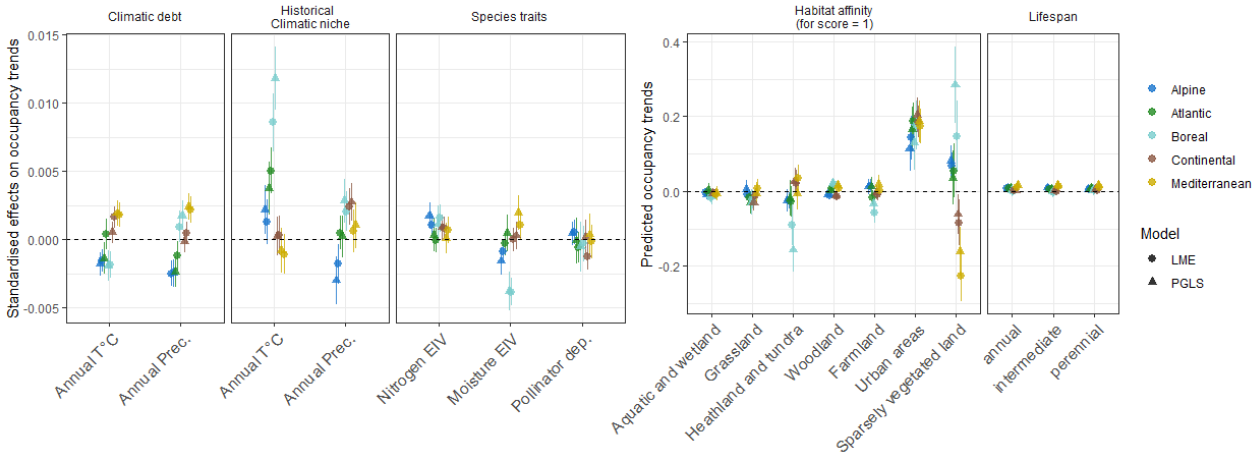


Figure S6: ***Occupancy trends from 1951 through 1990 and their correlation with SCI trends.*** *Estimates (±$CI_{95\%}$) from phylogenetic regressions (PGLS) and linear mixed-effect models (LME) explaining occupancy trends with temporal trends in SCI and other species traits.*



<u>Figure S7:</u> Occupancy trends and their correlates for each biogeographic region. *The three left panels represent the estimates (±$CI_{95\%}$) from PGLS and LME, explaining occupancy trends with temporal trends in SCI and other species traits. The two right panels show predicted averaged occupancy trends (±$CI_{95\%}$) for each habitat, considering a theoretical perfect affinity to each habitat (score = 1 & lifespan = annual), and for lifespan categories, predicting at the average of all other variables.*

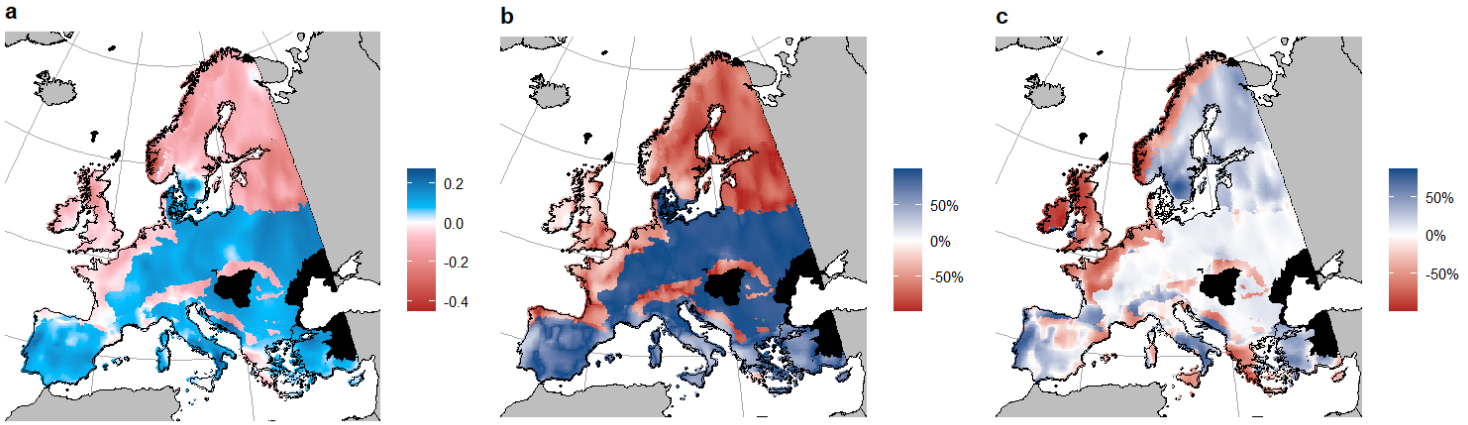


Figure S8: ***Climatic debt/bonus in Europe and its climatic drivers, considering non-significant predictors.*** *Same figure as Figure 4 of the paper but also considering effects of SCI trends that are not significant. (a) Climatic debt/bonus averaged over all species over the last 65 years. The gradient from white to red indicates a climatic debt (cost of climate change in terms of species occupancy), while the gradient from white to blue indicates a climatic bonus (benefits of climate change in terms of species occupancy); white represents no cost on average for plants. Relative contribution of (b) temperature and (c) precipitations SCI trends to the climatic debt, in percentage. Black regions are biogeographic regions with too few data. The maps were generated using predicts averaged over both models, LME and PGLS.*

Table S1 (separate file):
SCI, occupancy trends and species traits for the 4,120 species studied + the 58 invasive species present in the initial species list.

Table S2: EUNIS habitat classification, and the grouped habitat classification used in the study.

EUNIS categories	Our categories
A - Marine habitats	Aquatic and wetland
B - Coastal habitats	Aquatic and wetland
C - Inland surface waters	Aquatic and wetland
D - Mires, bogs and fens	Aquatic and wetland
E - Grasslands and land dominated by forbs, mosses or lichens	Grassland
F - Heathland, scrub and tundra	Heathland and tundra
G - Woodland, forest and other wooded land	Woodland
H - Inland unvegetated or sparsely vegetated habitats	Sparsely vegetated land
I - Arable land and market gardens	Farmland
J - constructed, industrial and other artificial habitats	Urban areas

Appendix IV

Duchenne F., Thébault E & Fontaine C. Disentangle phenotypic plasticity and evolution in phenotypic shifts: is competition driving pollinator flight period shifts? *In prep.*

Disentangling phenotypic plasticity and evolution of phenotypic shifts: is competition driving pollinator flight period shifts?

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Keywords: trait | phenology | adaptation | insect | opportunistic data

Paper type: Research article

Data accessibility statement: If the manuscript is accepted, the data supporting the results will be archived in a public repository and the data DOI will be included at the end of the article.

Abstract

Increasing evidence shows that climate change affects various phenotypic traits of species, such as the seasonal timing of biological events. However, whether the underlying mechanisms of these phenotypic changes involve phenotypic plasticity, evolution or both remain widely overlook, probably because it requires time consuming and costly population monitoring. Here we propose to use a statistical partitioning of phenotypic plasticity and evolution of phenotypic shifts, using historical data without information about pedigree or fitness that are usually used to do so. Using simulations and a known bird breeding phenology case study, we show that our method gives consistent estimate of phenotypic plasticity and evolution. Studying shifts in the mean flight date of pollinators in Great Britain, we find that their long-term mean flight date shifts are likely driven by evolution rather than by phenotypic plasticity to temperature. Moreover, integrating these flight period changes at a community level, we show that this evolution of mean flight date could be driven by competition pressures. Such results echoes theoretical ones and provide new elements to understand what mediate species responses to global change.

Introduction

Climate change strongly affects environmental conditions experienced by living organisms (Pachauri *et al.* 2014), increasing extinction risks for many species (Thomas *et al.* 2004). To persist in a such changing world, species can respond adaptively, by changing their phenotype to maintain an adequate match with the environment (Radchuk *et al.* 2019) or by tracking their climatic optimum spatially (Lenoir & Svenning 2015). Among phenotypic shifts due to climate warming, phenological shifts – i.e. shifts in the seasonal timing of life-cycle events – are largely documented (Parmesan 2006, 2007) and can be seen as a third axes of species responses to climate change, species tracking their optimum in time (Bellard *et al.* 2012). Those phenological shifts have been evidenced for a wide diversity of species as species response to climate change (Parmesan 2006, 2007), but mechanisms involved in such mechanisms remain widely overlooked.

Trying to disentangle the mechanisms driving phenological shifts is a key challenge to understand the effect of global change on evolutionary trajectories of species. Shifts of an average trait value of a species in response to an environmental variable can be due to two distinct mechanisms: phenotypic plasticity (Charmantier *et al.* 2008), and evolution including the evolution of plasticity (Asch *et al.* 2013; Govaert *et al.* 2016). Phenotypic plasticity is known to allow following faster the shift of optima than evolution (Chevin, et al., 2010), because it does not require the time-consuming process of the natural selection on heritable variations. However, while phenotypic plasticity can increase population persistence if it is adaptive (Charmantier *et al.* 2008; Chevin *et al.* 2010), it can also lead to developmental traps if it is maladaptive (Dyck *et al.* 2015). Moreover, as phenotypic plasticity can induce limited phenotypic change, evolution seems required to face long-term environmental changes and to maintain species (Visser 2008). This highlights the importance to assess the relative contribution of plastic and evolutionary responses to global change to assess future evolutionary trajectories of species and possibilities of evolutionary rescue.

However, the contribution of such mechanisms in observed phenotypic changes is rarely assessed, partly because it needs heavy and costly experimental studies (Merilä & Hendry 2014). Evaluate evolution requires information on the genetic relationships among individuals of the monitored population, or to have access to the historical population via dormant eggs or seeds (Stoks *et al.* 2016), or to realize common garden experiments (Merilä & Hendry 2014), or to develop genetic molecular approaches (Merilä & Hendry 2014). In contrast phenotypic plasticity can be easily estimated, by regressing the phenotypic values against the relevant environmental values (Nussey *et al.* 2007; Phillimore *et al.* 2010). This method to assess the phenotypic plasticity is based on the reaction norm concept (Fig. 1), which describes phenotype as a function, linear or not, of one or several environmental variables. Considering a linear function, the phenotypic plasticity corresponds to the slope of this function. It can be estimated by using a linear regression explaining the phenotypic values by the

environmental values. Previous studies have further shown that linear mixed-effects can be used to estimate both the plasticity and evolution of phenological shifts when they are combined with fitness measure or experiments (Brommer *et al.* 2012; Asch *et al.* 2013). The evolution of phonological shifts are then characterized by temporal changes in the elevation and/or the slope of the reaction norm. Similarly, the reaction norm concept was used to infer local adaptation in phenological events from occurrence and environmental data only, by comparing phenotype-environment relationships over time and over space (Phillimore *et al.* 2010; Roy *et al.* 2015). Those studies pave the way to use species occurrence date coupled with environmental data to infer evolutionary mechanisms of observed phenotypic changes, this without fitness measurements nor information about the matrix of additive genetic variances and covariances of the reaction norm parameters (G matrix). Since, long-term datasets monitored populations, with information about pedigree of individuals, remain scarce and available only for few taxa, such as birds or plants, developing these approaches to analyses phenotypic data only seems a key challenge.

Moreover, in addition to the difficulties to determine the mechanisms driving phenological shifts, the actual drivers of phenological shifts are also uncertain. Some studies suggest that phenological shifts are strongly and directly driven by climate (Roy & Sparks 2000; Hodgson *et al.* 2011), but others suggest that they can also lead to drive species decline through changes in inter-specific interactions, such as competition (Alexander & Levine 2019; Carter & Rudolf 2019). As a consequence, phenological shifts are sometimes presented as an adaptive response to track the climatic optimum of species (Tansey *et al.* 2017) and sometimes as a threat for species and communities (Edwards & Richardson 2004; Hegland *et al.* 2009). Such paradoxical views on phenological shifts are difficult to unify in a consistent framework mainly because of uncertainties regarding the drivers and mechanisms involved. Depending on whether phenological shifts are driven or not by interspecific interactions, we expect different consequences for communities (Loeuille 2019; Rudolf 2019) as well as depending on whether phenological shifts involve phenotypic plasticity and/or evolution we expect different consequences for species persistence (Chevin *et al.* 2010). Indeed, if evolution is involved in phenological shifts, it makes evolutionary rescue possible for species (Carlson *et al.* 2014), and if evolution allows maintaining species interactions, it can prevent community collapse (Loeuille 2019).

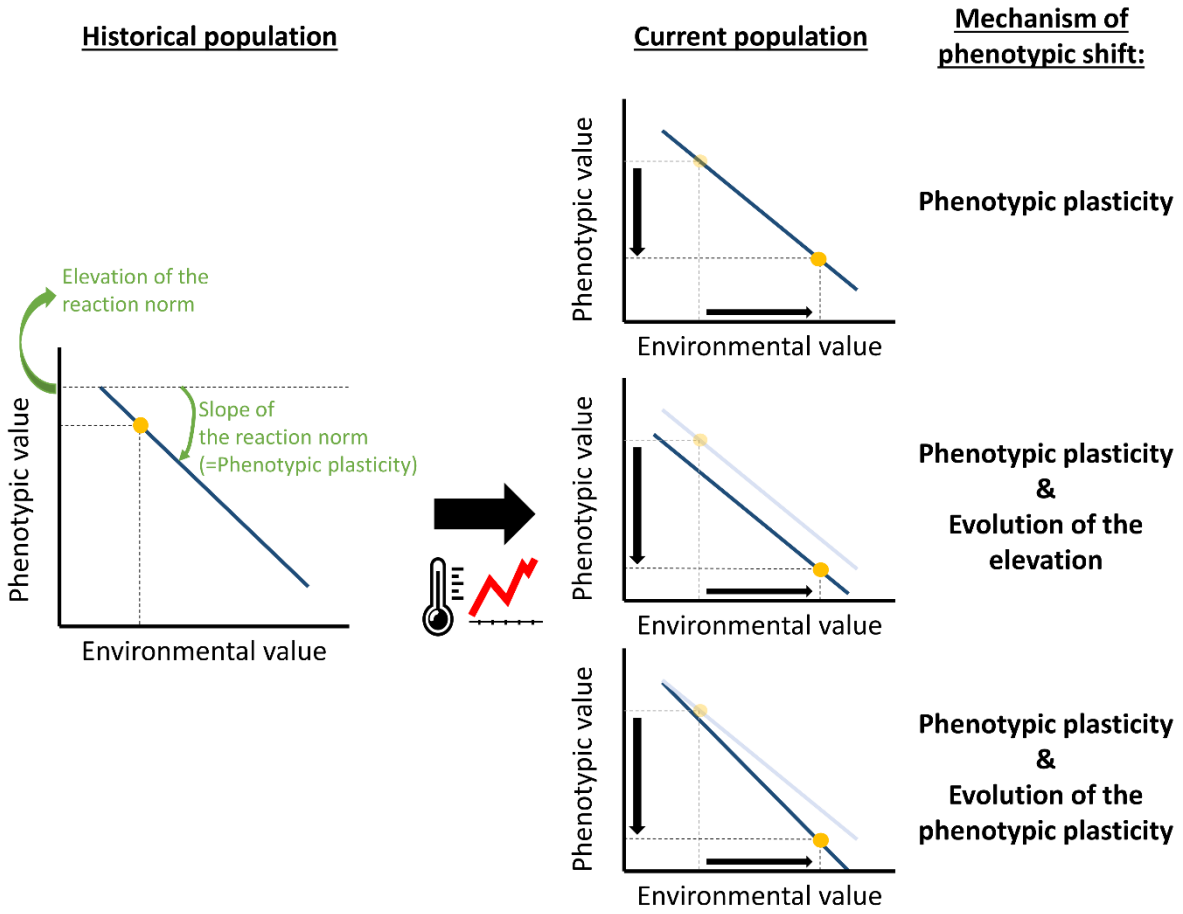


Figure 1: ***Schematic example of phenotypic change because of climate warming seen from the reaction norm concept****. All the possible phenotypic values are represented as a linear function of an environmental variable (blue line). This representation can regard either one individual or the average values of a population. For a given environmental value, there is one possible phenotypic value (yellow dot), since we neglected the residual variation. The reaction norm includes two parameters (in green), the elevation and the slope (i.e. the phenotypic plasticity), both able to evolve. If an environmental change occurs, phenotype can change because of phenotypic plasticity only, or because of phenotypic plasticity and evolution. In the latter case evolution can occur in the elevation or in the slope or in both (not represented here for simplicity). Black arrows along axes represent shifts in environmental conditions (x-axis) and in phenotype (y-axis), while shaded lines and dot represent historical reaction norm and phenotype value respectively.*

Historical opportunistic datasets, containing only presence data with a species name, a date, a location and sometimes with incomplete data about collectors, are often the only historical data source for many taxa. When analyzed with appropriate statistical methods, such dataset can give important temporal information (Isaac *et al.* 2014; Bartomeus *et al.* 2019). Those historical datasets were used to characterized phenological shifts, such as pollinator and plant flight/flowering period shifts (Roy & Sparks 2000; Bartomeus *et al.* 2011; Robbirt *et al.* 2011; Hassall *et al.* 2017). Although these phenological shifts have been linked to temperature changes (Bartomeus *et al.* 2011) and we know that pollinator flight period is plastic with respect to temperature (Valtonen *et al.* 2011; Fründ *et al.* 2013; Roy *et al.* 2015; Forrest 2016), evolutionary responses driven by inter-specific interactions, such as

competition (Carter & Rudolf 2019; Loeuille 2019; Rudolf 2019), are widely neglected. Consequently, we still know little about the drivers, abiotic *vs* biotic, and the mechanisms, phenotypic plasticity *vs* evolution, of pollinator flight period shifts, while it is a key knowledge to understand the consequences of phonological shifts for species persistence and species assemblages. Here, we test whether linear models can allow assessing the relative contributions of phenotypic plasticity and evolution using both simulated data and data already analyzed with classical methods. We then use this method on a large dataset of pollinator occurrences, from 1960 to 2016 over the Great-Britain, to fill an important gap in the understanding of underlying mechanisms of phenotypic shifts in response to climate change, studying pollinator flight period shifts over time.

Methods

Our goal was to estimate the contribution of phenotypic plasticity and evolution in the mean flight date shifts of pollinators in Great-Britain, and link those contributions with changes in the seasonal structure of pollinator assemblages. To do so, we propose to use linear model on an opportunistic dataset to partition the part of mean flight date shifts due to temperature and corresponding to the phenotypic plasticity to temperature, and the part due to an independent year effect interpreted as a signal of evolution. To do so, we first test our method by evaluating the conditions required to assess changes in reaction norm parameters (elevation and slope) with linear models, by using simulated data with known values of changes in reaction norm parameters. We also compared results obtained with a linear model to those obtained with an animal model on a dataset previously published (Ramakers *et al.* 2019). Second, we estimated the contribution of phenotypic plasticity and evolution in pollinator mean flight date shifts. Third, we assessed how mean flight date shifts due to phenotypic plasticity and those due to a putative evolution affect the seasonal structure of pollinator assemblages in Great-Britain.

Estimate reaction norm parameters by using linear models

As often done in the quantitative genetic studies, we used a model based on the reaction norm concept describing a phenotypic value *z*, averaged over a population, as a function of the environment (Scheiner 1993; Nussey *et al.* 2007; Chevin & Lande 2011):

$$z = a + b\varepsilon + e \quad (1)$$

where a is the average elevation of the reaction norm of the population, corresponding to the phenotypic value in the reference environment ($\varepsilon = 0$) and b is the average phenotypic plasticity of the population (the slope of the reaction norm) to the environmental variable value ε and e a normally distributed residual component of variation following $\mathcal{N}(0, \sigma_e^2)$. This equation is similar to a linear equation model, making plasticity easily assessable by estimating the parameters of this equation by regression approaches (Nussey *et al.* 2007; Asch *et al.* 2013). Such model can be extended to a phenotypic plasticity

to multiple environment variables, but for simplicity here we assume that our phenotype depends only on one environmental variable.

In the following part, we used an evolutionary framework, from Chevin & Lande (2011). Starting with the equation (1), we can define covariance matrix (G) of reaction norm parameters (a and b): $G = \begin{pmatrix} Gaa & Gab \\ Gab & Gbb \end{pmatrix}$, where Gaa is the variance of a, Gbb is the variance of b and Gab the covariance between a and b. As empirical estimation of Gab on bird breeding phenology does not significantly differ from zero (Ramakers *et al.* 2019), we simplified the model by considering a and b as independent parameters and thus setting $Gab = 0$. Moreover, we considered a fixed covariance matrix (G) of reaction norm parameters, as its erosion due to directional selection in natural population remains uncertain (Roff & Mousseau 1999; Waldmann 2001; Wehenkel & Sáenz-Romero 2012). Then, we assume that there is an optimal phenotypic value (z_{opt}), that also depends on the environmental variable ε: $z_{opt} = a_{opt} + b_{opt} \times \varepsilon$, where a_{opt} is the optimal phenotypic value in the reference environment ($\varepsilon = 0$), and b_{opt} is the sensitivity of the optimal phenotypic value to the environment. If $b_{opt} = 0$, then the phenotypic value is insensitive to the environment variable ε. As shown by Chevin & Lande (2011), we can thus define a fitness function (W):

$$W = \exp\left(-\frac{(z - z_{opt})^2}{2\omega}\right) \quad (2)$$

The fitness (W) associated to each phenotype (z) decreases as the distance with the optimal phenotypic value (z_{opt}) increases. ω is the width of the fitness function, which determines partially the strength of selection. Then assuming discrete and non-overlapping generations and infinite population size, we can simulate the evolution of the reaction norm parameters between generation *t* and *t+1* by using the fitness gradient and the covariance matrix (G), following Chevin & Lande (2011):

$$\Delta P_t = \frac{-1 \times (z_t - z_{opt})}{\omega^2 + \sigma_z^2} \times G \times \begin{pmatrix} 1 \\ \varepsilon \end{pmatrix} \quad (3)$$

$$\begin{pmatrix} a_{t+1} \\ b_{t+1} \end{pmatrix} = \begin{pmatrix} a_t \\ b_t \end{pmatrix} + \Delta P_t \quad (4)$$

where the vector ΔP_t contains additive evolutionary values of the reaction norm elevation and slopes, respectively added to a_t and b_t to define the reaction norm parameters of the next generation, a_{t+1} and b_{t+1}. The phenotypic variance $\sigma_z^2 = \begin{pmatrix} 1 \\ \varepsilon \end{pmatrix} \times G \times (1, \varepsilon) + \sigma_e^2$.

Representing the evolution of the phenotype iteratively among generations can be represented as follow:

$$z_t = a_t + b_t\varepsilon + e \tag{5}$$

$$z_{t+1} = a_t + \Delta_{a_t} + \left(b_t + \Delta_{b_t}\right)\varepsilon + e \tag{6}$$

$$z_{t+2} = a_t + \Delta_{a_t} + \Delta_{a_{t+1}} + \left(b_t + \Delta_{b_t} + \Delta_{b_t+1}\right)\varepsilon + e \tag{7}$$

$$z_{t+n} = a_t + \sum_{j=t}^{t+n-1} \Delta_{a_j} + \left(b_t + \sum_{j=t}^{t+n-1} \Delta_{b_j}\right)\varepsilon + e \tag{8}$$

Where Δ_{a_j} is the evolution of the elevation between generations *j* and *j*+1, and Δ_{b_j} is evolution of the phenotypic plasticity between generations *j* and *j*+1. As fitness gradient vary over time, Δ_{a_j} and Δ_{b_j} are not constant terms but vary among generations, but we can define average evolution rates of *a* and *b* over *n* generations, $\overline{\Delta_{a_n}}$ and $\overline{\Delta_{b_n}}$ respectively: $\overline{\Delta_{a_n}} = \frac{1}{n}\sum_{j=t}^{t+n-1} \Delta_{a_j}$ and similarly for $\overline{\Delta_{b_n}}$. Then we can write the equation (8) as follow:

$$z_{t+n} = a_t + \overline{\Delta_{a_n}} \times n + \left(b_t + \overline{\Delta_{b_n}} \times n\right)\varepsilon + e \tag{9}$$

In this equation, a_t is the ancestral elevation of the reaction norm (at time *t*), b_t is the ancestral phenotypic plasticity, $\overline{\Delta_{a_n}}$ is the evolution rate of the elevation of the reaction norm and $\overline{\Delta_{b_n}}$ is the evolution rate of the phenotypic plasticity.

Again, the equation (9) is similar to the equation of a linear model. Thus, if we have a time-series of phenotypic values and of the environmental variable (ε), assuming that the time is proportional to the number of generations, we can estimate the unknown parameters (a_t, b_t, $\overline{\Delta_{a_n}}$ and $\overline{\Delta_{b_n}}$) using the following linear model:

$$z_{ti} = \beta_0 + \beta_1 \times time_t + (\beta_2 + \gamma \times time_t) \times \varepsilon + e_{ti} \tag{10}$$

Where z_{tk} is the phenotypic value at time *t* for observation *i*, β_0 is the elevation (a_t), β_1 a time effect estimating $\overline{\Delta_{a_n}}$, β_2 the environmental variable effect estimating b_t and γ is the interaction among time and the environmental values estimating $\overline{\Delta_{b_n}}$. e_{ti} is an error term normally distributed, independent and following $N(0,\sigma^2)$. Thus, we propose here to use such linear model to estimate ecological and evolutionary process contribution in phenotypic changes over time.

Test of the method on simulated data

To assess how linear models perform in parameter estimations we used simulations derived from the model presented above. We know that estimations of reaction norm parameters by using linear models should be sensitive to the correlation between time and environmental variable, to the number of records and to the length of the studied time series. Thus, we applied variations in those variables in

simulations. For the simulations, we take the example of a pollinator population, where the studied phenotype is the mean flight date of a population. We started simulation with a population in the reference environmental value ($\varepsilon = 0$), ε being a temperature variable for example. Thus, at t = 0, the phenotypic value equals the elevation of the reaction norm ($z = a + e$). As said above, we considered a constant G matrix over time within each simulation, in which Gaa is sampled in a uniform law from 1 to 5, $U(1, 5)$, for each simulation while Gbb is sampled in a $U(0.5, 2)$ for each simulation. Since we do not have any information about G matrix in pollinators, we considered a higher range of variance on the elevation than on the slope of the reaction norm, consistently to what was observed in bird laying date (Ramakers *et al.* 2019).

We considered one generation by year, and we simulated trait evolution for a given number of years (n_t), from 25 to 55, depending on the simulation. Each year t a new value of ε was drawn from a Gaussian distribution following $\mathcal{N}(0.015 \times t, \sigma_\varepsilon^2)$, to simulate an environmental change over time. Since the average temperature increase is fixed over simulations, for a given number of years, σ_ε^2 determines the variations in the correlation between the years and the environmental change, and thus the directionality of the selection. The higher it is, the lower the correlation between time and the environmental value is. We expected that this correlation will strongly affect our ability to estimate independently changes in the reaction norm parameters, and thus we simulated for distinctive values of σ_ε^2, from 0.03 to 0.5, to change such correlation between time and the environmental variable. Then for each year we defined the phenotypic value (z_t) using equation (1) and we simulated an observation process, by drawing observations of pollinator from $\mathcal{N}(z_t, \sigma_{Z_t}^2)$. As the number of observations will affect our estimation power, we also simulated for distinctive total number of observations (n_{obs}), from 500 to 2,500, spread on n_t years. Other numerical values used for the simulation are presented in Table 1.

Table 1: *parameters values used for the simulation.*

Parameter	Meaning	Value
$a_{t=0}$	Initial elevation of the reaction norm (day of the year)	180
$b_{t=0}$	Initial slope of the reaction norm (Phenotypic plasticity, day/°C)	$\sim U(-6, 6)$
ε_t	Environmental value (°C)	$\sim \mathcal{N}(0.015 \times t, \sigma_\varepsilon^2)$
σ_ε^2	Variance of the environmental variable	0.03/0.05/0.07/0.1/0.15 /0.2/0.25/0.3/0.4/0.5
Gaa	Variance of a_t, fixed over time	$\sim U(1, 5)$
Gbb	Variance of b_t, fixed over time	$\sim U(-0.5, 2)$ / 0
Gab	Covariance of a_t and b_t, fixed over time	0
a_{opt}	Initial optimal phenotypic value (day of the year)	180
b_{opt}	Sensitivity of the optimal phenotypic value to the environment (day/°C)	$\sim U(-6, 0)$
ω	Width of fitness function	$\sqrt{5}$
σ_e^2	The variance of the residual phenotypic variation	7
n_t	Number of years (=generation) of the simulation	25/30/35/40/45/50/55
n_{obs}	Number of total observations	500/1000/1500/2500

We run 2,000 simulations for each combination of number of data, number of years and σ_ε^2, with evolution of phenotypic plasticity ($Gbb \sim \mathcal{N}(0.5,2)$) and without it ($Gbb = 0$), leading to 1,120,000 simulations in total. For each simulation we apply the linear model presented in equation (10) to estimate β_0, β_1, β_2 and γ that we compare with a_t, $\overline{\Delta_{a_n}}$, b_t, and $\overline{\Delta_{b_n}}$, respectively. As the evolution of phenotypic plasticity is estimated by a linear interaction term between the time and the environmental value, it is the less robust estimation probably not always estimable with real data, we also estimated β_0, β_1, β_2 by using a linear model without interaction term between temperature and time. Such method allows assessing what are the consequences of neglecting the evolution of phenotypic plasticity for the estimation of other parameters.

Empirical test of our method

We found only one available empirical datasets allowing to compare our method with classical estimation from selection gradients (Ramakers *et al.* 2019). Ramakers *et al.* (2019) analysed the breeding time of Great tits (*Parus major*) on a long-term dataset (1969-2016) from a monitored population. Using an animal model to estimate the G matrix, they estimated directional selection pressures on the elevation and on the slope of the reaction norm (Ramakers *et al.* 2019).

We applied our method to their dataset, using the linear model presented in the equation (8) but adding a year random effect to account for different number of records per year and for residual inter-annual variation in the laying date around the linear trend. Then we compared our estimates with what they found.

Pollinator database

We applied our method to pollinator flight period shifts, a well-known response to climate change (Roy & Sparks 2000; Bartomeus *et al.* 2011; Hassall *et al.* 2017; Duchenne *et al.* 2020). To do so, we used part of the dataset from Duchenne *et al.* (2020), which gathers occurrence records of pollinator from 1960 to 2016 in Europe, regarding 4 order of insects: Diptera, Hymenoptera, Coleoptera and Lepidoptera. We considered only records from Great Britain, because it is the most sampled area, with relatively homogenous climatic conditions, all the Great Britain belonging to the Atlantic biogeographic region. Following Duchenne et al. (2020) we split multimodal flight periods in unimodal ones and studied them separately because they can react to the different environmental variables. Because simulations show that a minimum number of records and number of years with records is needed to use our method (Fig. 2), we considered only species with at least 50 records on 1960-1989 and 500 records on 1990-2016. This leads to a list of 767 unimodal flight periods, henceforth phenologies, regarding 675 species and a dataset of 9,547,555 million of occurrences, with a strong over representation of Lepidoptera as in the original dataset.

Selection of climatic indices

Phenology of pollinators, and especially of Lepidoptera that represent the majority of our dataset, strongly depends on temperature, but not at the same period of the year for all species (Roy & Sparks 2000; Bale & Hayward 2010; Roy *et al.* 2015). Thus, to be able to describe as well as possible phenotypic plasticity to temperature we considered several temperature indices. For each records we extracted temperature on 1960-2016 at 0.1° of precision in WGS84, using the R package *climateExtract* (Schmucki n.d.). Then we calculated average temperature on windows of 90 days, moving the beginning of the window by 30 days on the 0 - 360 interval. Windows overlapping two years, those beginning from the day of the year 300 and after, were associated to the year of the end date of the window.

Then, for each species independently we used a linear mixed-effect model to explain the day of the year of pollinator observations by temperature indices and by a grid cell effect to model the known spatial variation in pollinator flight period (Hodgson *et al.* 2011). Grid cells used here to model spatial distribution of records are 50km×50km. We included a maximum of 3 temperature indices in this model to avoid overfitting, but we performed one model for each possible combination of temperature indices including from one to three indices, excluding combination of temperatures indices with more than 30 days of overlap. The linear mixed-effect models used can be described as follow, for a model including three temperature indices:

$$DY_{ijm} = \beta_0 + \left(\beta_1 + \Delta\beta_{1_m}\right) \times temp1_j + \left(\beta_2 + \Delta\beta_{2_m}\right) \times temp2_j + \left(\beta_3 + \Delta\beta_{3_m}\right) \times temp3_j + \theta_m + \varphi_j + e_{ijm} \quad (11)$$

where DY_{ijs} is the day of the year of observation *i* belonging to grid cell *m* and to year *j*, β_0 is the intercept, β_1, β_2 and β_3 are the respective effects of temperatures indices. $\Delta\beta_{1_m}$, $\Delta\beta_{2_m}$ and $\Delta\beta_{3_m}$ are random effects of the grid cell on each temperature indices effects. θ_m is a random grid cell effect on the intercept and φ_j is a random year effect to model residual inter-annual variations. Finally, e_{ijm} is an error term; random terms are all expected to be independent, identically distributed, and homoscedastic.

Then we selected the model with the lowest Akaike Information Criterion (AIC), considered as the model including temperature indices that determine the best the phenotypic plasticity of the species flight period.

Application of our method on pollinator mean flight date shifts

Once temperature indices determining phenotypic plasticity has been selected, for each species we applied the previously selected linear mixed-effects model, but adding a fixed year effect to the equation (11), to estimate simultaneously the phenotypic plasticity to temperature indices and the remaining temporal trend, considered as a proxy of the directional selection:

$$DY_{ijm} = \beta_0 + \left(\beta_1 + \Delta\beta_{1_m}\right) \times temp1_j + \left(\beta_2 + \Delta\beta_{2_m}\right) \times temp2_j + \left(\beta_3 + \Delta\beta_{3_m}\right) \times temp3_j + \theta_m + \varphi_j + \left(\beta_4 + \Delta\beta_{4_m}\right) \times year_j + e_{ijm} \quad (12)$$

where β_4 is the year effect and $\Delta\beta_{4_m}$ is a random effect of the grid cell on the year effect. Thus, in this model we have a fixed year effect to model linear temporal trend and a random year effect to take into account the heterogeneous distribution of records among years and account for residual inter-annual variations in mean flight date. However, in the following part, we analyzed only the fixed year effect, since it should correspond to the estimation of evolution of mean flight date, while the random effect is not of interest.

Looking for seasonal and spatial patterns in phenotypic plasticity and year effect

As insect phenology shifts exhibit a spatial and a seasonal heterogeneity as well as a phylogenetic signal (Hodgson *et al.* 2011; Duchenne *et al.* 2020), we looked for seasonal, spatial and taxonomical heterogeneity in estimated phenotypic plasticity, corresponding to the $\beta_{1\ldots3}$ of the equation (12), and in estimated year effect, corresponding to the β_4 from the equation (12). To do so, we used linear mixed effect models, modelling the phenotypic plasticity estimates by average latitude and longitude of species records, neglecting altitude as it exhibits very few inter-specific variations, and their seasonal earliness (i.e. average mean flight date). To take into account phylogenetic relationships among species, we added order and family random effects. Thus, for the year effect we used the following model:

$$YE_{ofs} = \beta_0 + \beta_1 \times latitude_s + \beta_2 \times longitude_s + \beta_3 \times elevation_s + \beta_4 \times \overline{mfd}_s + \theta_o + \theta_f + e_{ofs} \quad (13)$$

where YE_{ofs} is the year effect on mean flight date of species *s*, from order *o* and family *f*. β_0 is the intercept, β_1, β_2, β_3 and β_4 are the respective effects of latitude, longitude, elevation and seasonal earliness ($\overline{mfd}$). β_5 and β_6 are the polynomials effects of the end date of the temperature indices ($T.date$). θ_0 and θ_f are taxonomical random effects of order and family respectively. Finally, e_{ofs} is an error term, expected to be independent, identically distributed, and homoscedastic.

Regarding phenotypic plasticity, we used a similar model than presented in equation (13), but with some modifications. Since for each species we have selected one, two or three temperature indices, we can have different number of phenotypic plasticity estimates, with respect to different temperature indices. Moreover, since response to temperature is susceptible to exhibit a nonlinear seasonal pattern, we added a polynomial effect of degree 2 of the date of the three-month temperature index, modelling the fact that species do not react in the way to different temperature indices. Moreover, as this seasonal pattern in phenotypic plasticity is susceptible to vary among spring and autumn species, we added an interaction between the seasonal earliness and this polynomial effect. Finally, to take into account the fact that all species do not have the same number of phenotypic plasticity estimates, we added a species random effect. Thus, we used the tow following model for phenotypic plasticity:

$$PP_{ofsd} = \beta_0 + \beta_1 \times latitude_s + \beta_2 \times longitude_s + \beta_3 \times elevation_s + \beta_4 \times \overline{mfd}_s + \left(\beta_5 + \gamma_1 \times \overline{mfd}\right) \times T.date_d + \left(\beta_6 + \gamma_2 \times \overline{mfd}\right) \times T.date_d^2 + \theta_o + \theta_f + \theta_s + e_{ofsd} \quad (14)$$

where PP_{ofsd} is phenotypic plasticity of mean flight date of species *s*, from order *o* and family *f*, to temperature indices *d*. β_5 and β_6 are the polynomials effects of the end date of the temperature indices ($T.date$). θ_s is a species random effect and e_{ofsd} is an error term, expected to be independent, identically distributed, and homoscedastic.

Since PP_{ofsd} and YE_{ofs} were estimated through a model, equation (12), to account for their associated errors, both models were weighted by the square root of the invert of associated standard errors.

Relative contributions of phenotypic plasticity and independent year effect

Since estimates of phenotypic plasticity are in days/°C and the year effect in day/year, they are not comparable. To be able to estimate their relative contributions to long-term mean flight date shifts we multiplied the phenotypic plasticity estimates by the temporal trend of the associated temperature indices, which gives a contribution phenotypic plasticity in day/year to mean flight date shifts (CPP). To do so, we estimated temporal trend in temperature indices using the following linear mixed-effects model for each species and each temperature indices associated (i.e. included in the model presented in equation (12)):

$$T_{ijm} = \beta_0 + \left(\beta_1 + \Delta\beta_{1_m}\right) \times year_j + \theta_m + e_{ijm} \quad (15)$$

where T_{ijm} is the temperature associated with species observation *i* from grid cell *m* and from year *j*. Julian day of the observation *i* belonging to the grid cell *m* and to the year *j*, β_0 is the intercept, while $\beta_1$is the temporal trend of the temperature indices. Finally, e_{ijm} is an error term expected to be independent, identically distributed, and homoscedastic.

However, as we can have several phenotypic plasticity estimate by species, we had to sum all *CPP* of each species to have a measure comparable to the year effect obtained in equation (12). We also calculated the relative contributions of phenotypic plasticity and year effect in overall mean flight date shifts. Relative contribution of phenotypic plasticity (in %) is calculated as follow:

$$RCPP = \frac{|\sum_1^n CPP_n|}{|YE| + |\sum_1^n CPP_n|} \times 100 \quad (16)$$

where *n* is the number of temperature indices associated to the species, C_{pp_n} the contribution of their associated phenotypic plasticity values and YE the contribution of the year effect, which is simply the year effect from equation (12). The relative contribution of the year effect ($RCYE$) is thus 1-RC_{PP}.

Finally we study seasonal and spatial patterns of the relative contribution of the year effect using the same model than the one presented in equation (13) but changing the response variable and using a generalized linear mixed-effect model with a binomial error distribution to work on the logit of the relative contribution, because it is percentage.

Characterizing changes in the seasonal structure

Phenological shifts can lead to changes in the seasonal structure of species assemblages (Diez *et al.* 2012; CaraDonna *et al.* 2014; Theobald *et al.* 2017; Carter *et al.* 2018; Duchenne *et al.* 2020), by changing species that co-occur in time along the season. To investigate how both the phenotypic plasticity and the year effect affect the seasonal structure of species assemblages, we estimated how the average overlap among phenologies has change over time. To do so, we modeled phenologies by Gaussians. The mean of the Gaussian (i.e. the mean flight date) is predicted using the model presented in equation (12), for each species and each combination of year and grid cell with records of the given species. The standard deviation of the Gaussian (i.e. the flight period length), is calculated for each grid cell as the standard deviation of residuals of the model associated to the given grid cell. Thus, it is a measure corrected by phenological shifts and space, but fixed over time to avoid calculating it on few data only. We calculated those phenological overlaps over time using mean flight date predictions based only on phenotypic plasticity or based on phenotypic plasticity and the year effect. For these two sets of predictions we calculated the same overlap among each species pairs for each year and each grid cells and then we averaged this index to get one value by species by grid cell by year ($\overline{OV_{mj}}$). To get the effect of the year effect only on overlap among phenologies, we make the subtraction of overlap got by using predictions considering only phenotypic plasticity minus overlap got by using predictions considering phenotypic plasticity and year effect.

Finally, we looked for temporal trend in this difference of overlap indices ($\Delta\overline{OV_{mj}}$) by using the following linear mixed-effect model for each species, taking into account the location of grid cells by latitude and longitude effects and by a random grid cell effect. We also accounted for the variation in the temporal trend among grid cells by a random effect on the temporal slope:

$$\Delta\overline{OV_{mj}} = \beta_0 + (\beta_1 + \Delta_m) \times year_j + \beta_2 \times latitude_m + \beta_3 \times longitude_m + \theta_m + \varphi_j + e_{mj} \qquad (17)$$

where $\Delta\overline{OV_{mj}}$ is the overlap among phenologies in grid cell *m* and to year *j*, β_0 is the intercept, β_1 is the temporal trend. β_2 and β_3 are effects of the latitude and the longitude of the centroid grid cell, respectively. θ_m is grid cell random effect and Δ_m is a random effect of the grid cell on the slope β_1. e_{mj} is an error term; random terms are all expected to be independent, identically distributed, and homoscedastic. This model was fitted only for species with at least 3 grid cells with at least 150 phenologies in at least 5 years, other combination of grid cell and year being considered as under

prospected. The slope β_1 from equation (17), thus give us the temporal trend in overlap among phenologies due to the year effect of equation (12), considered as a signal of evolution.

Results

Numerical and empirical test of our method

As, expected we find that the precision of our method strongly depends on the number of years of the time-series and on the correlation between time and the environmental variable (Fig. 2). However, we show here, that our dataset contains combinations of phenological time-series associated with temperature indices that meet requirements for estimating the parameters of the reaction norm with relatively small errors (Fig. 2). Longer time-series with more observations, as well as lower time-temperature correlations, lead to more precise parameter estimations. Although our simulation include a stochastic observational process, we show that our method allows reliable estimations of evolution ($\overline{\Delta_{a_n}}$) and phenotypic plasticity (b_t) when the latter does not evolve ($\overline{\Delta_{b_n}} = 0$, Fig. S1). When we performed simulations including evolution of the phenotypic plasticity, as both, time and temperature effects become non-independent and not linear, our estimations of the evolution appear slightly biased, but still strongly correlated with simulated values (Fig. S2). Thus, despite the absolute values of estimators for cases with strong evolution of reaction norm elevation seems a bit overestimated when phenotypic plasticity is evolving, estimated values are still highly correlated with simulated values and intercept of the relationship is not biased (i.e. very close to zero, Fig. S2). This suggests that our method can still be used to detect estimate evolutionary mechanisms in phenotypic shifts. We also show that neglecting the evolution of phenotypic plasticity by removing the interaction between the time and temperature does not induce a strong bias in our estimations (Fig. S3), suggesting that out method is robust to the fact that there could be neglected mechanisms affecting the phenotype (i.e. evolution of phenotypic plasticity).

Moreover, our method gives results consistent with those from an animal model, when applied on a published dataset (Ramakers *et al.* 2019). We find a significant time effect on the Great tits laying date, -0.0815 ± 0.037 day/year (mean ± s.d.e), suggesting a directional selection on the elevation of the reaction norm. This estimation gives a cumulative advancement of the laying date because of evolution of the reaction norm elevation of -3.91 [-7.38,-0.44] days (mean [$CI_{95\%}$]) that is consistent with estimate found by Ramakers et al. (2019) using a quantitative genetic model, -2.34 [-4.20, -0.48] days. In parallel we estimated a phenotypic plasticity of -2.919 ± 0.338 day/°C, also consistent with the findings of the quantitative genetic model, -3.28 [-3.92,-2.68] day/°C. As Ramakers et al. (2019), we did not find any evidence for a significant evolution of the phenotypic plasticity, -0.0052 ± 0.020 day/°C/year. Thus, in a system where the environmental variable determining the phenotypic value is well known our method

give highly consistent results with those of a classical quantitative genetic model, but without estimating the G matrix, allowing to apply it on phenotypic data only.

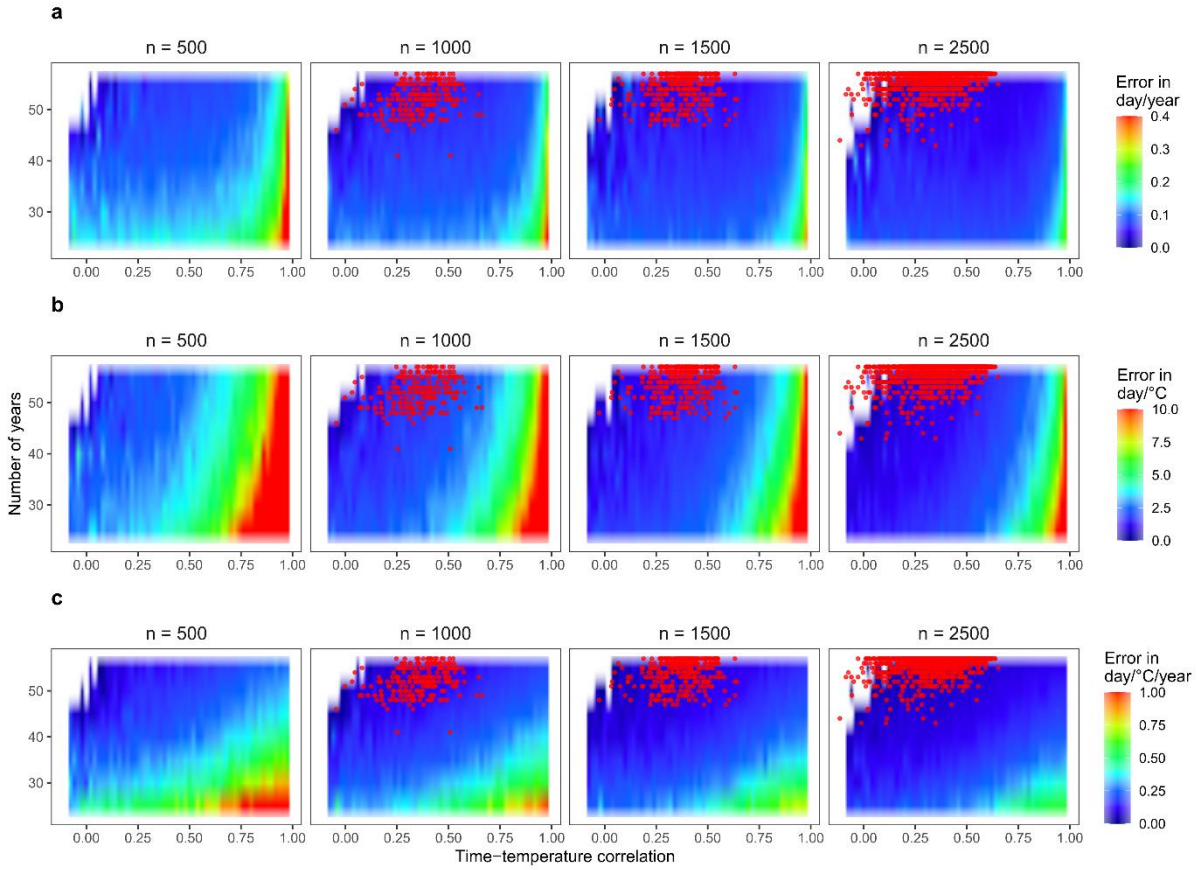


Figure 2: ***maximum error on the parameter estimation as a function of the time-temperature correlation, the number of year of the time-series (n_t) and of the number of total records simulated (n_{obs}).*** *For (a) estimations of evolution of the elevation of the reaction norm ($\overline{\Delta_{a_n}}$), (b) estimations of phenotypic plasticity (b_t), and (c) estimations of the evolution of phenotypic plasticity ($\overline{\Delta_{b_n}}$), for a case where $\overline{\Delta_{b_n}}$=0. Maximum error is the 95% quantile of the distribution of the absolute value of errors, for each number of years (from 25 to 55 by 5 years), and for each interval of 0.02 of time-temperature correlation, and patterns were linearly interpolated. Color scales were truncated on their upper limit to preserve readability, blue colors correspond to low errors and red colors to high levels of error on parameter estimation. White areas correspond to areas without simulations. Red points correspond to the distribution of empirical values from the pollinator dataset, for each combination of species and selected temperature indices.*

Plasticity in pollinator flight period shifts

We find that time-temperature correlation was never higher than 0.65, suggesting that our method should not be biased as our dataset has at least 41 years of observations for all species included (Fig. S1). We show that the mean flight date is significantly correlated with three temperature indices for 22% of phenologies (i.e. unimodal flight periods), with two indices for 40% of the phenologies and with one index for 32% of the phenologies. This shows that the flight period of many pollinator species is plastic to the climatic conditions of multiple periods in the year. This phenotypic plasticity of pollinator flight period to temperature exhibit a strong seasonal heterogeneity: while species advance their mean flight

date in response to an increase in spring temperature, they tend to delay their mean flight date in response to an increase in temperature at the ends of the season, during the previous winter and during autumn (Fig. 3a). Such seasonality significantly further depends on earliness of species, earlier species being more plastic in general and advancing more their mean flight date in response to temperature increase in spring than latter ones (Fig. 3a). Spring temperatures affect more species' flight periods than winter or autumnal temperatures (Fig. 3b). This phenotypic plasticity does not exhibit any latitudinal or longitudinal patterns, between southern/northern or eastern/western species, and it is poorly explained by the taxonomical random effects, suggesting that it is not strongly linked to the evolutionary history.

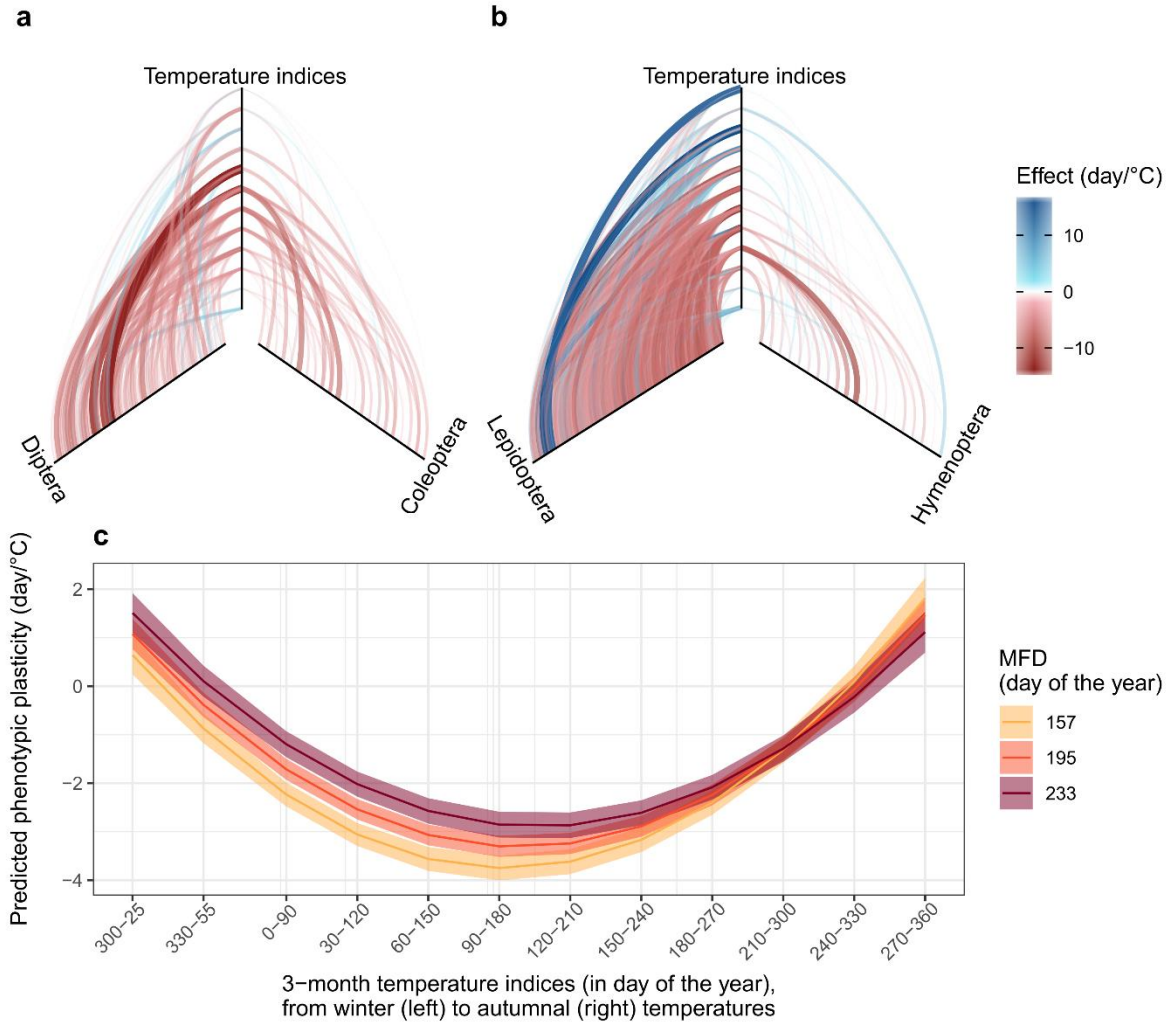


***Figure 3:* seasonal variation in the strength of phenotypic plasticity to temperature.** *Hive plots of phenotypic plasticity to temperature indices for (a) Diptera & Coleoptera and for (b) Lepidoptera and Hymenoptera. Temperature indices are ordered from winter (bottom) to autumnal indices (top) in the same order than in (c). For each taxonomical order, species are ordered by seasonal earliness, form earliest (origin of the axis) to latest species (end of the axis). (c) Predicted values of phenotypic plasticity in function of the date of the 3-month temperature indices used (end date of indices) and of the seasonal earliness (i.e. the mean flight date, MFD). Middle lines show predictions while ribbons show 95% confidence interval.*

A year effect independent from the phenotypic plasticity

We detect a significant temporal trend in the pollinator mean flight date, independent from the phenotypic plasticity for 323 (45%) of the studied phenologies. Surprisingly, this linear year effect is more often positive than negative (Fig. 4a), suggesting that it participate to delay or to reduce the advance of the mean flight date over time. This year effect exhibits a significant relationship with the seasonal earliness of species (χ^2 = 7.88, p-value = 0.005), early species having a negative year effect while latter species tend to have a positive one (Fig. 4b). We do not find any significant latitudinal or longitudinal gradients among species, but in contrast to phenotypic plasticity the random effect of taxonomic order explains 5% of the variance, suggesting differences among orders, mainly due to the fact that Hymenopterans have a more negative year effect than other orders (Fig. S4).

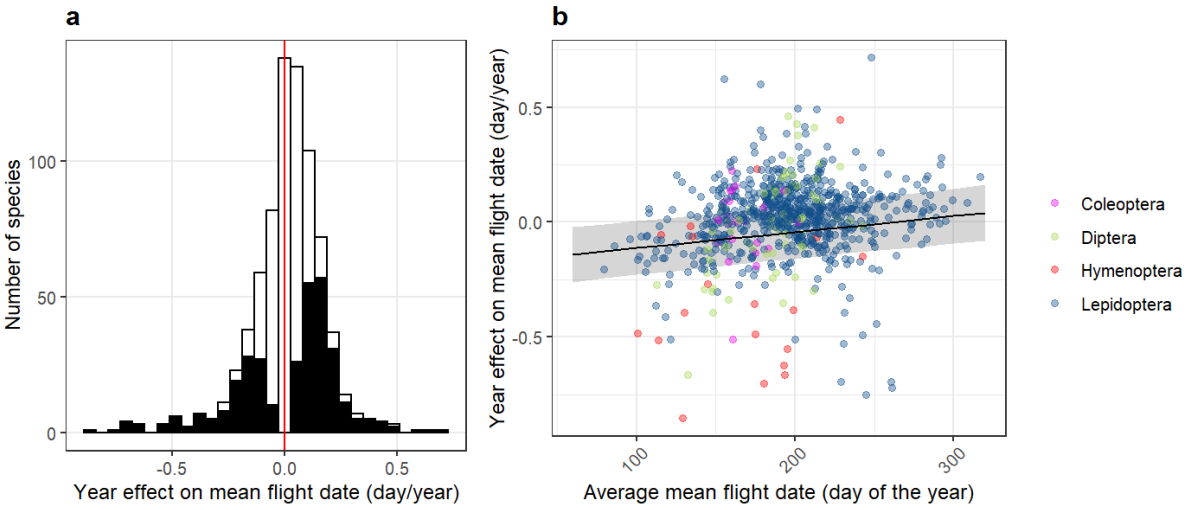


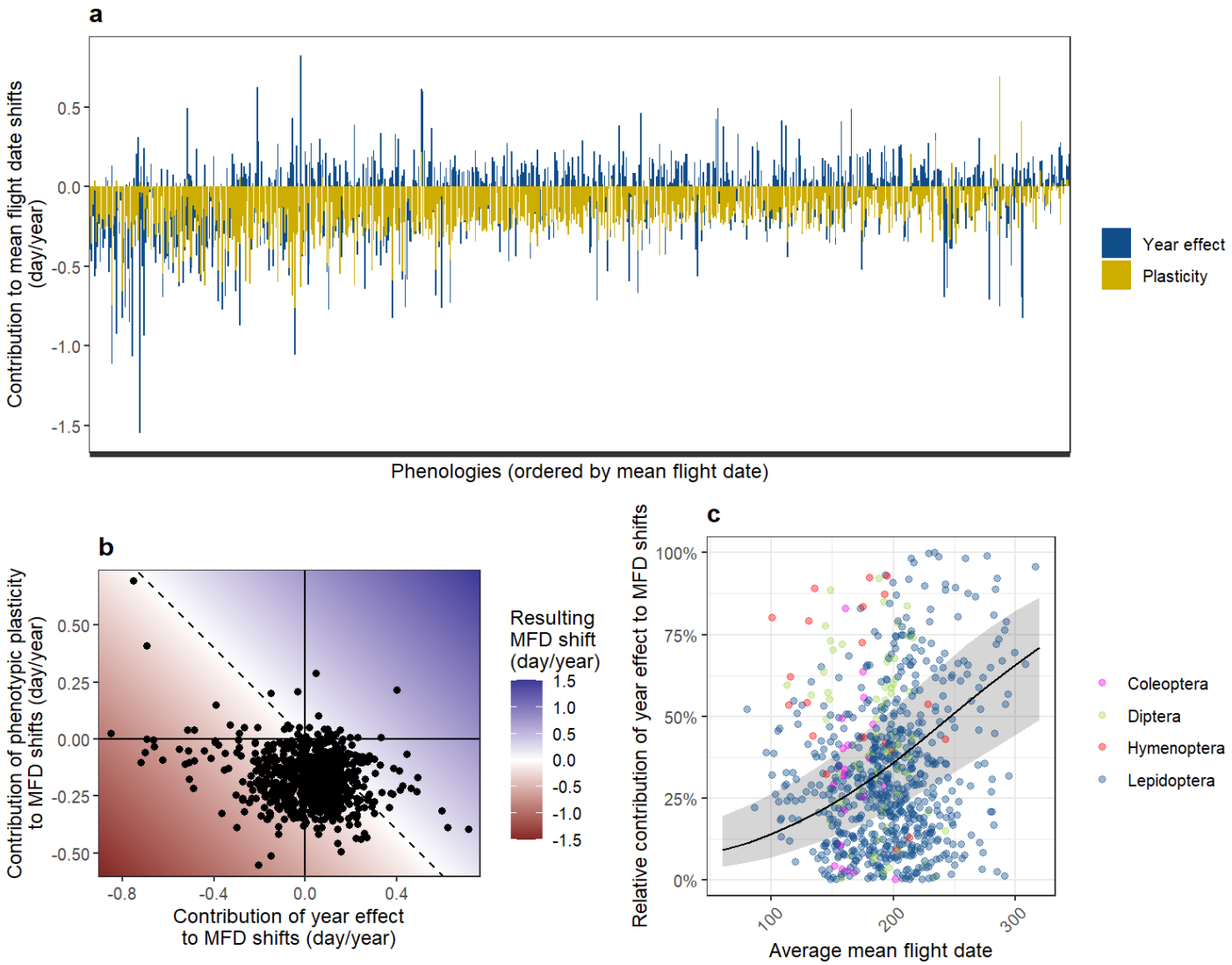
Figure 4: ***linear fixed year effect, independent from phenotypic plasticity, on pollinator mean flight date.*** *(a) Histogram of year effect (i.e. temporal trend) in mean flight date. Filled bars represent significant estimates (p-value < 0.05) while open bars represent non-significant ones (p-value > 0.05). The red vertical line shows the zero value. (b) Year effect on mean flight date in function of the seasonal earliness (average mean flight date) and of the order. The black line shows the predictions from model presented in equation (14) while ribbon shows the 95% confidence interval.*

Contributions of phenotypic plasticity and year effect in mean flight date shifts

By quantifying the contributions of phenotypic plasticity and constitutive adaptation in the long-term mean flight shifts, we find that the phenotypic plasticity tends to advance the mean flight date by -0.173 ± 0.004 days/year in average, because of temperature increase, while the average year effect on the mean flight date is 0.013 ± 0.006 days/year. Thus, the year effect contributes to advance less the mean flight date than expected by phenotypic plasticity alone (Fig. 5a-b), or even to delay the mean flight date for end-season species with low phenotypic plasticity to temperature (Fig. 5a).

Focusing on relative contributions, we also show that phenotypic plasticity to temperature is the main contributor to long-term mean flight date shifts, as it contributes to 64% in average in mean flight date shifts. However, there is a non-negligible year effect, which contributes to 36% in average in long-term pollinator mean flight date shifts. Again, there is a strong seasonal pattern, with the relative

contribution of the year effect on the mean flight date shifts that increase from spring to autumn (χ^2 = 50.16, p-value = 1.42e-12, Fig. 5c), mainly because end-season species have a low contribution of phenotypic plasticity in mean flight date shifts (Fig. 5a). We do not find any significant spatial pattern but a strong taxonomical signal, mainly driven by Hymenoptera. The relative contribution of the temporal trend independent to the mean flight date shifts is higher in Hymenoptera (77% ± 7, mean ± s.d.e) and Diptera (45% ± 4) than in Coleoptera (26% ± 4) and Lepidoptera (35% ± 1).



<u>Figure 5:</u> contributions of phenotypic plasticity and the year effect to long-term pollinator mean flight date shifts. *(a) Bar plot of contributions for all species ordered from the earliest to the latest one. (b) Contributions of the year effect (i.e. temporal trend independent from phenotypic plasticity) in function of contributions of phenotypic plasticity to mean flight date shifts. Background color represents the resulting mean flight date (MFD) shifts when adding both contributions. (c) Relative contribution of the year effect to MFD shifts in function of the seasonal earliness (average mean flight date) by order. The black line shows the predictions from linear mixed-effect model while ribbon shows the 95% confidence interval.*

However, as the variance among species of the phenotypic plasticity contributions (0.011) is weak, because phenotypic plasticity is almost always negative, it does not explain the long-term mean flight

date shifts variation among species. Indeed, the heterogeneity in long-term mean flight date of pollinators are much better explained by the contributions of year effect to mean flight date shifts (Fig. S5), which are much more variable (variance = 0.024) than the phenotypic plasticity.

Consequences for the seasonal structure of species assemblages

By estimating for each species in each grid cells and for each year the overlap with other phenologies, we were able to estimate the temporal trend in phenological overlap. We estimated the contribution of the year effect in this temporal trend in phenological overlap, by comparing the temporal changes in overlap when considering plastic changes of the mean flight date only, or when considering both, plastic and time-correlated changes (i.e. year effect) in the mean flight date. We find a significant average negative temporal trend of -1.36e-4 ± 1.7e-5 (p-value = 3.7e-15) over all species, indicating that phenological shifts due to the year effect tend to decrease the overlap among phenologies over time. The year effect on mean flight date significantly decreases the temporal trend in average overlap for 227 phenologies (30%) while it significantly increases the temporal trend in average overlap for 82 phenologies only (11%, Fig. 6a). This year effect on temporal trend of overlap tend to be slightly more negative for species with high values of average overlap, corresponding to species at the core of the pollination season (Fig. 6a), but the relationship is not significant (Fig. 6b).

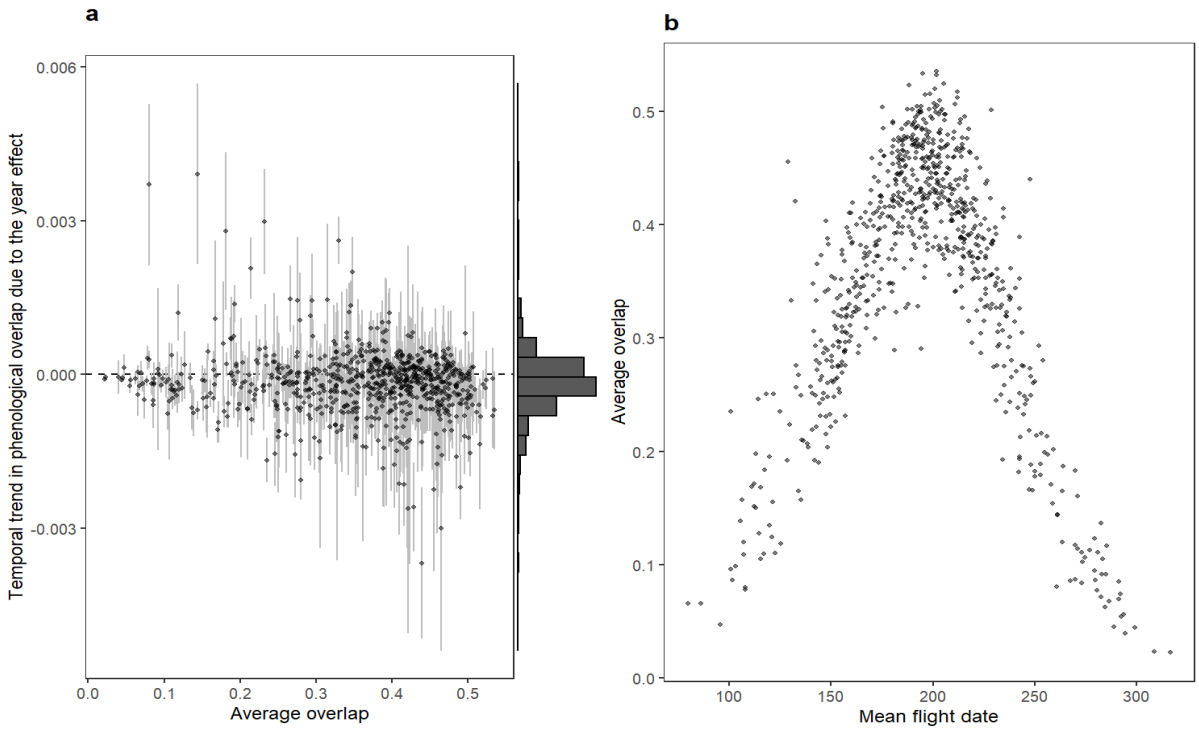


Figure 6: ***Temporal trends in overlap due to year effect in function of average overlap among phenologies.*** *(a) Temporal trend in overlap among phenologies due to year effect for each species, against their average overlap among phenologies over all years. Red line is the prediction of a linear model weighted by the invert of associated error standards while ribbons represent 95% confidence interval. (b) Average overlap against mean flight date (seasonal earliness) for each species.*

Discussion

In the first part of this paper, we show that using time series of phenotypic records only, linear models can be used to estimate the contribution of phenotypic plasticity and evolution to phenotypic variation over time. Even when neglecting the evolution of phenotypic plasticity, our estimations of plasticity and evolution remain consistent. An important point is that as the evolution is estimated by a year effect independent from the phenotypic plasticity to the chosen environmental variable, our method requires to know toward which environmental variable the phenotype is plastic. Neglecting an important environmental variable in the phenotypic plasticity could lead, if such environmental variable is at least partially correlated with the time, to interpret its effect as evolution. Thus, the method used here is not a substitute of transplantation experiments or animal models, as both have much more power and less bias to infer evolution because they infer trait heritability and associated fitness, two primordial measures to estimate selection gradient and evolution. However, our method allows inferring some information from occurrence data, regarding traits for which plastic responses are well understood, such as phenological traits. Indeed the phenotypic plasticity of birds' breeding phenology or flight period of insects are well characterized, both responding to temperature and day length (Nussey *et al.* 2007; Charmantier *et al.* 2008; Visser *et al.* 2009; Bale & Hayward 2010; Gienapp *et al.* 2010; Valtonen *et al.* 2011; Roy *et al.* 2015; Forrest 2016). Because day length does not vary over years but solely over space, temperature should be the only driver of plastic phenotypic variations over time for such traits. Thus, regarding those traits, once phenotypic plasticity to temperature have been properly taken into account, the remaining temporal trend should be informative about evolutionary mechanisms affecting the studied phenotype.

Turning to the use of our approach to assess the eco-evolutionary mechanisms underlying long-term mean flight date shifts of pollinators, the estimation of phenotypic plasticity to spring temperature we found, -4.7 ± 0.14 day/°C from April to June, is consistent with previous estimations on British butterflies, -3.8 day/°C (Roy & Sparks 2000) and -6.4 day/°C (Roy *et al.* 2015). We also show that the plastic response to temperature is stronger for early species than for end-season species, consistently with previous results (Roy *et al.* 2015). The lower plastic response of end-season species could be because phenotypic plasticity can be maladaptive for these species (Dyck *et al.* 2015), likely due to the fact unfavorable climatic conditions in autumn are less predictable from earlier temperature than climatic conditions in spring/summer. End-season species may rely more on day length, a stable and more reliable environmental cue for autumn phenological events (Gallinat *et al.* 2015; Way & Montgomery 2015). Such decrease of the plastic response of species to temperature with their mean flight date could partly explain why end-season pollinator are advancing less their mean flight date on the long-term than earlier ones (Bartomeus *et al.* 2011; Duchenne *et al.* 2020).

We further show that differences of long-term mean flight date shifts among pollinators are mainly driven by a temporal trend, independent from the plastic response to temperature, and not by phenotypic plasticity. We suggest that this year effect is a signal of evolution. The fact that phenotypic plasticity alone does not explain long-term phenological shifts has also been found in avian migration timing (Buskirk *et al.* 2012) and is consistent with the fact that on the long-term, phenotypic plasticity alone is probably not enough to face climate warming (Visser 2008). Indeed, studies on flowering period of plants have shown that plant flowering shifts in response to climate warming are due to both phenotypic plasticity and evolution (Anderson *et al.* 2012) and increase plant fitness (Ehrlén & Valdés 2020). However, here, in contrast to results on shifts in flowering period, we find that the year effect is often opposite to plastic response, suggesting a counter-gradient between phenotypic plasticity and evolution. Such counter-gradients have already been found for about 60 species on various traits, including phenological traits of insects, but have been more often evidenced over space than time, and using experimental systems (Conover *et al.* 2009). Here we suggest that climate warming is leading to a strong counter-gradient between phenotypic plasticity and evolution of pollinator flight period, for a wide diversity of species. Such counter-gradient could be due to an adaptive evolutionary response on physiology to counteract effect of temperature increase on physiological processes.

Another mechanism leading to this counter gradient could involve inter-specific interactions creating a selection pressure to avoid competition with other pollinators or to access more floral resources. Such relationship between phenological shifts and the seasonal structure of species assemblages can be view in both direction: either phenological shifts drive changes in the seasonal structure, or the seasonal structure (i.e. inters-specific interactions) drives the phenological shifts. Importantly, such inversion of causality compared to the classical view, is however not incompatible with possible negative consequences on pollination function. Moreover, these two viewpoints are not incompatible, as they can constitute a feedbacks loop. One has to notice that the potential effect of inter-specific interactions driving phenology shift is rarely discussed. A decrease of overlap among pollinator phenologies that tend to belong to the same taxonomical group can lead to a decrease in functional redundancy, because they probably feed on the same flowers because of the phylogenetic signal in pollination networks (Rezende *et al.* 2007). Thus, the phenological overlap of species belonging to the same functional group can be linked to competition pressures, a decrease in their overlap decreasing competition pressures (Carter & Rudolf 2019; Rudolf 2019). We found that the decrease of the overlap among phenologies is driven by the possible evolution of mean flight date (i.e. year effect) rather than by the phenotypic plasticity to temperature. Such result suggests that competition among pollinators could be the driver of this adaptive evolution.

We acknowledge that phenological synchrony does not offer a perfect estimation of competition pressure, because competition depends also on pollinator and resources abundances as well as any other dimensions of their ecological niches. However, theoretical (Rudolf 2019) and empirical work (Carter

& Rudolf 2019) have shown that phenological synchrony is strongly linked to competition in ecological communities. If competition strongly mediates the consequences of phenological shifts for organisms, it probably involves a strong selection pressure on phenology and thus should be view as a driver, rather than as a consequence, of phenological shifts (Loeuille 2019). Competition is known to be non-negligible and even relatively important in mutualistic networks (Jones *et al.* 2012; Maeng *et al.* 2012), especially among pollinators (Henry & Rodet 2018). Thus, the fact that phenological shifts are mainly driven by competition and not by a direct response to temperature as often supposed, is consistent with theoretical and empirical knowledge on the link between phenology and competition in pollination networks. However, eco-evolutionary mechanisms remain widely overlooked in current species responses to global change and our study is the first piece of evidence that suggest a strong importance of evolutionary responses in current pollinator phenological shifts.

Although it is based on strong assumptions, we think that our approach is valuable when applied on phenotypic traits for which plastic determinism is simple and well known, and that it allows highlighting mechanisms of long-term responses to climate change, regarding taxa for which we do not have any monitored population scheme with pedigrees. Here, we suggest that historical data contains the trace of an evolutionary response of the pollinators' flight period shifts, potentially driven by competition, providing new elements to understand what mediate species responses to global change, a key question of ecology and evolution in a changing world.

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Supplementary

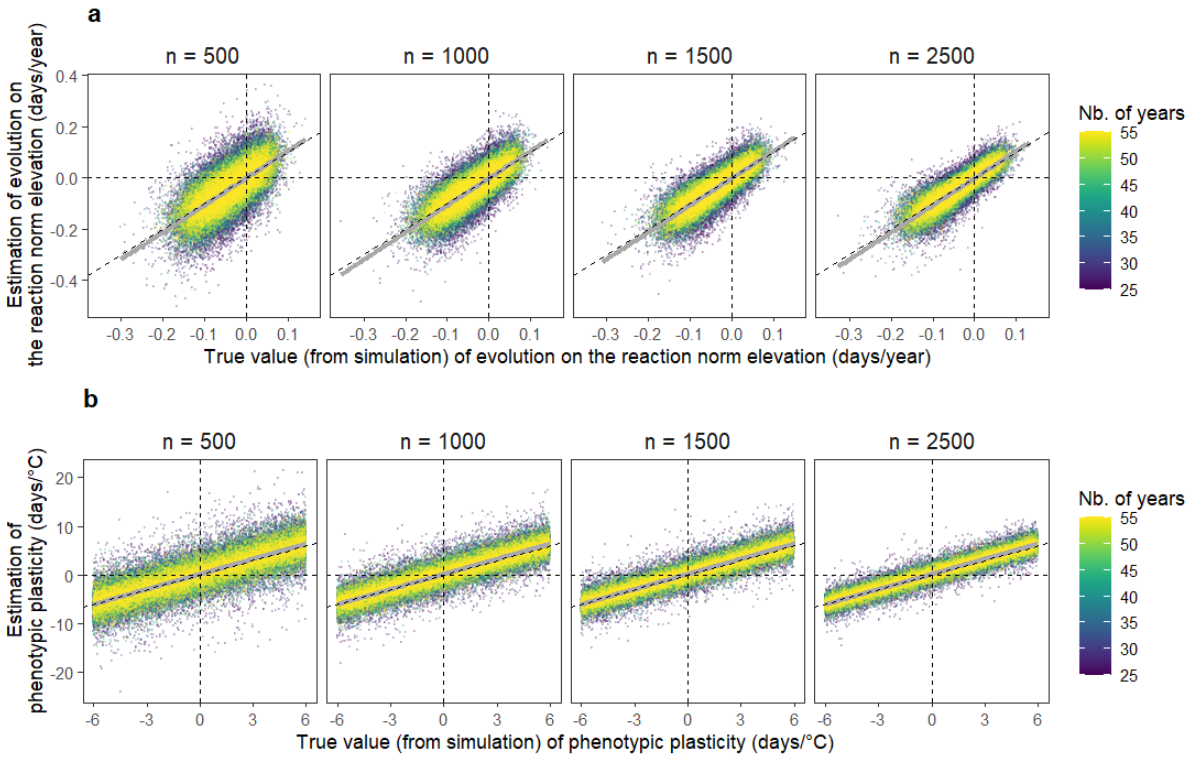


Figure S1: ***Relationships between estimated and simulated values of reaction norm parameters***. *For (a) evolution of the elevation of the reaction norm ($\overline{\Delta_{a_n}}$) and (b) phenotypic plasticity (b_t), and, for a case where there is no evolution of the phenotypic plasticity ($\overline{\Delta_{b_n}} = 0$). Dashed black lines represent zero values and the first bisector while the grey solid line represents the predict result of a linear model of the presented relationship. We used here only simulations with a time-temperature correlation higher than 0.2 and lower than 0.8.*

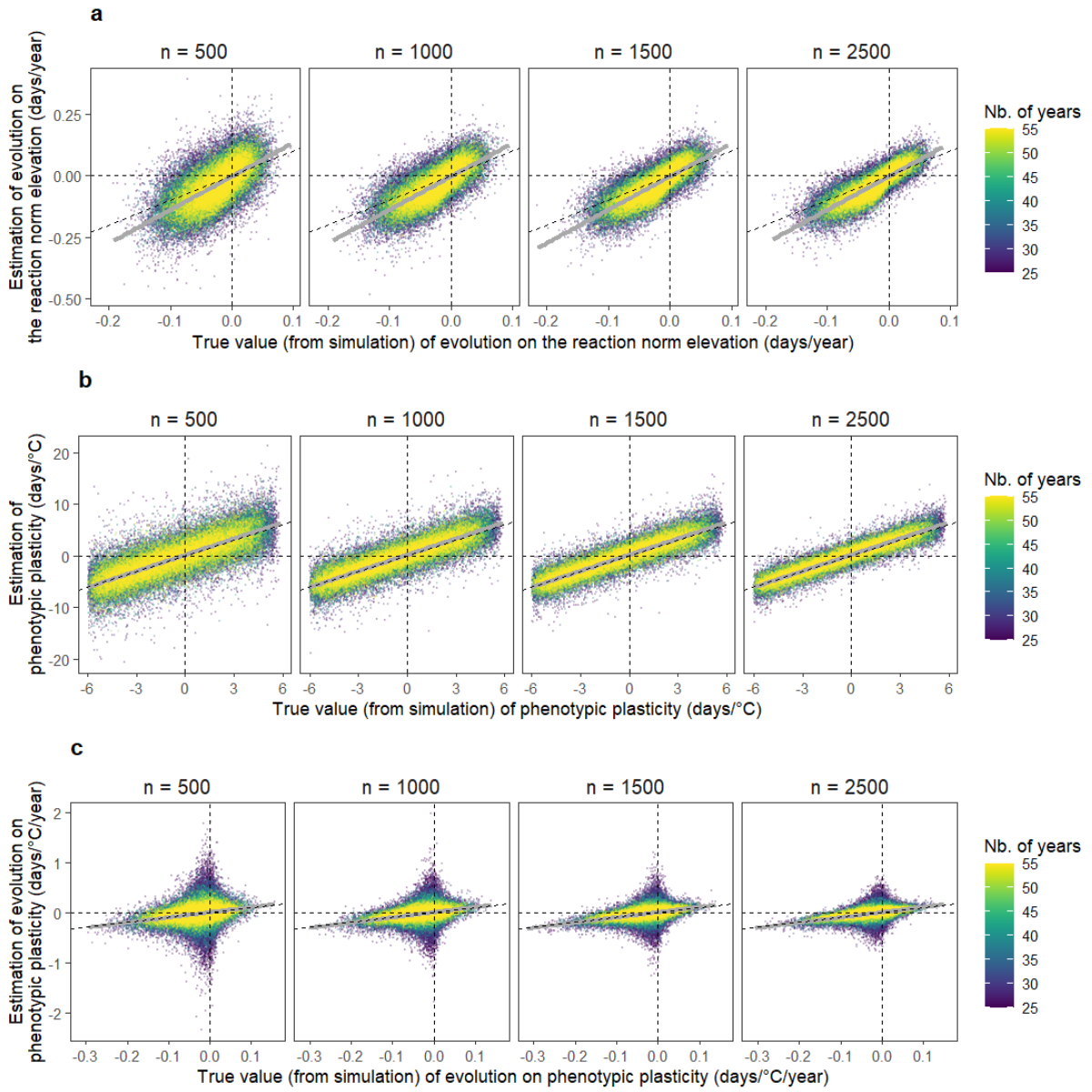
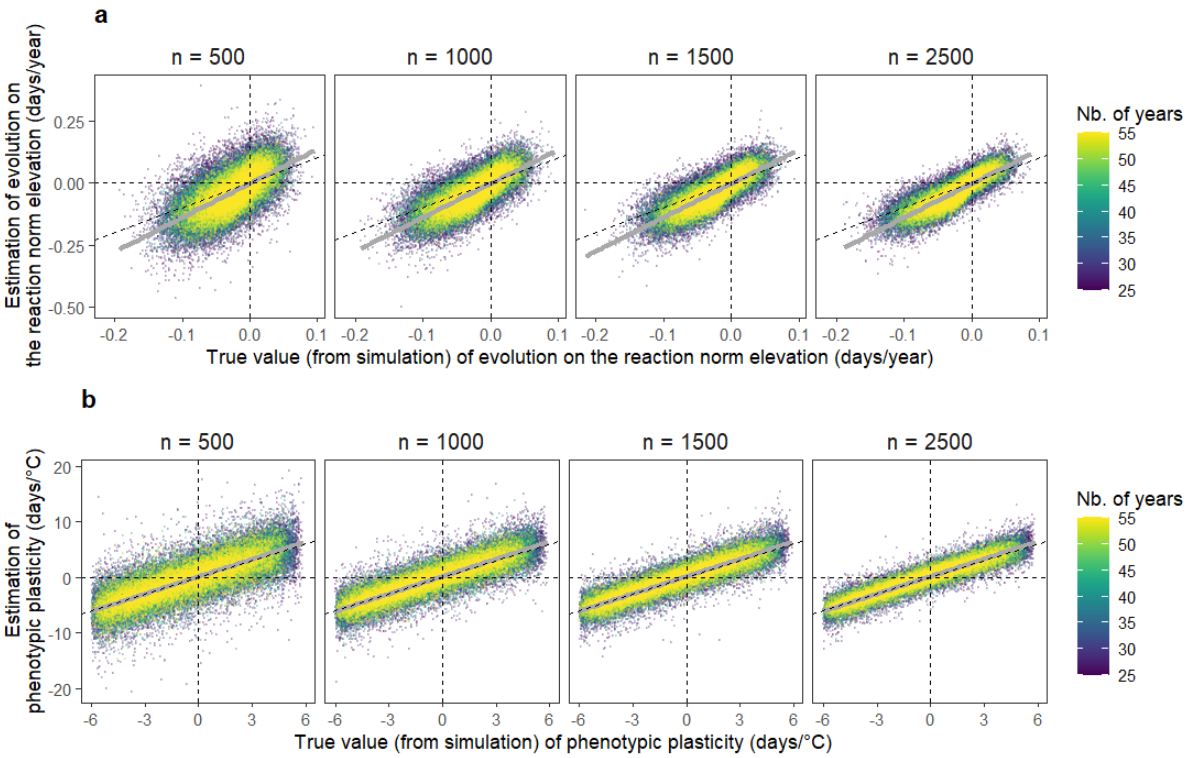


Figure S2: ***Relationships between estimated and simulated values of reaction norm parameters when phenotypic plasticity evolves***. *For (a) evolution of the elevation of the reaction norm ($\overline{\Delta_{a_n}}$) and (b) phenotypic plasticity (b_t), (c) evolution of phenotypic plasticity ($\overline{\Delta_{b_n}}$), for cases where we allow evolution of phenotypic plasticity. Dashed black lines represent zero values and the first bisector while the grey solid line represents the predict result of a linear model of the presented relationship. We used here only simulations with a time-temperature correlation higher than 0.2 and lower than 0.8.*



<u>Figure S3:</u> ***Relationships between estimated and simulated values of reaction norm parameters when phenotypic plasticity evolve but we neglected it in the estimation*** *For (a) evolution of the elevation of the reaction norm ($\overline{\Delta_{a_n}}$) and (b) phenotypic plasticity (b_t), for cases where we allow phenotypic plasticity evolution but we did not include an interaction between time and temperature in the linear model, thus we neglected phenotypic plasticity evolution. Dashed black lines represent zero values and the first bisector while the grey solid line represents the predict result of a linear model of the presented relationship. We used here only simulations with a time-temperature correlation higher than 0.2 and lower than 0.8.*

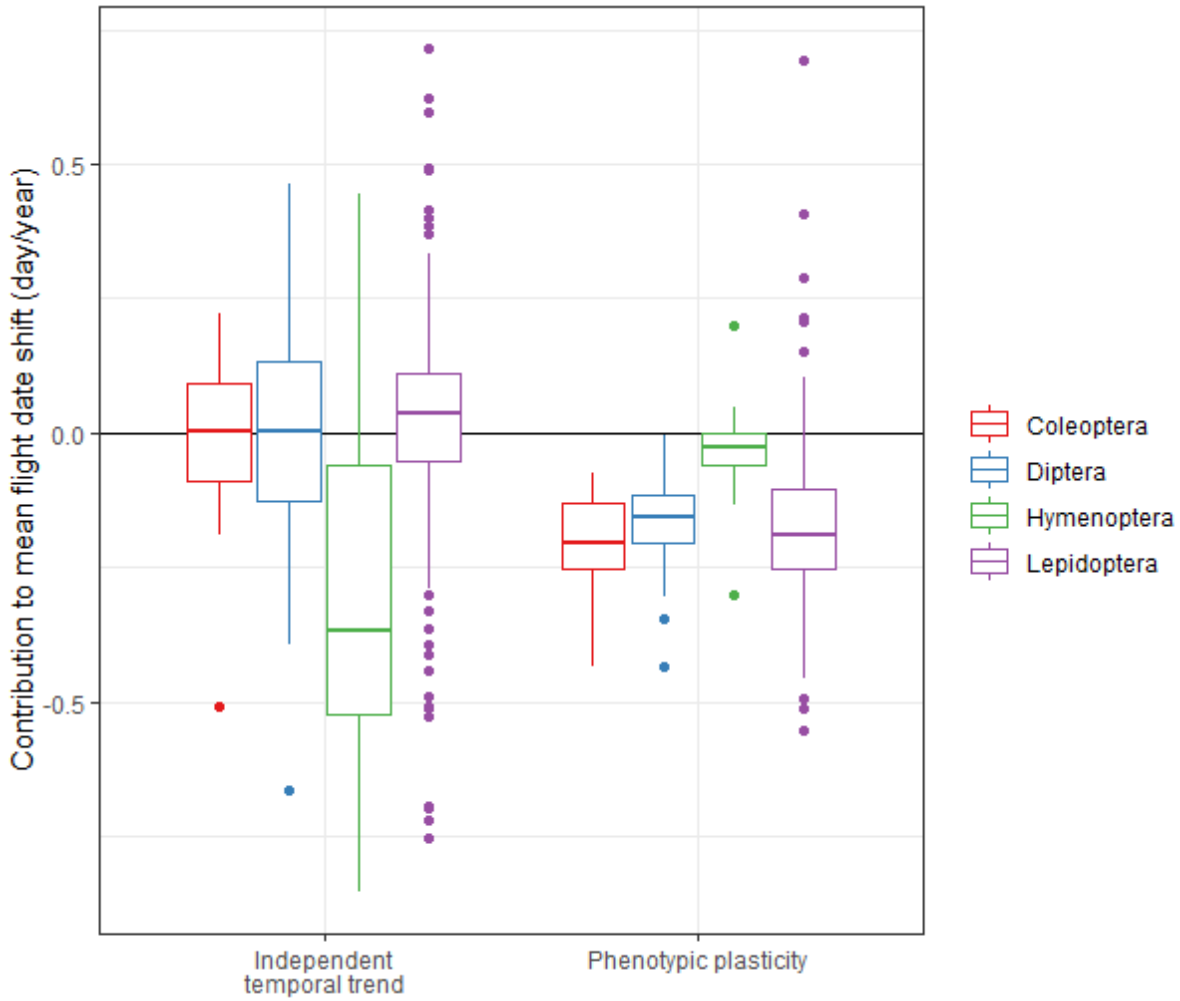


Figure S4: ***Contributions of phenotypic plasticity and independent temporal trend to mean flight shifts by order.***

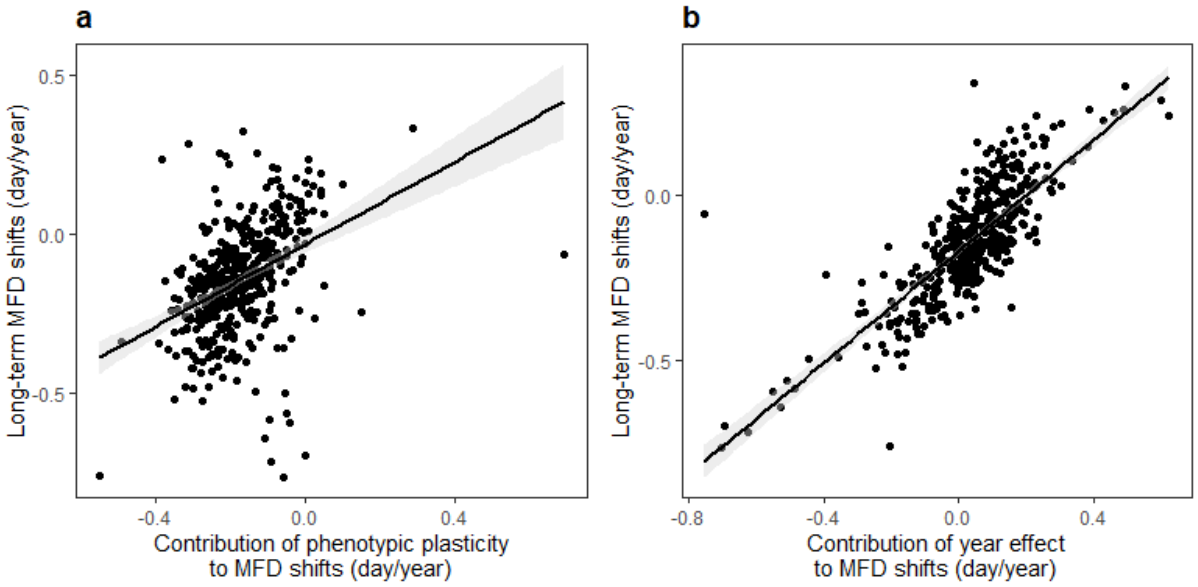


Figure S5: ***Long-term mean flight date shifts in function of the contributions of phenotypic plasticity and year effect****. Relationships between the long-term mean flight date (MFD) shifts and (a) the contribution of the phenotypic plasticity or (b) the contribution of the year effect (i.e. the temporal trend in MFD, independent form the phenotypic plasticity). Black lines represent the predictions of a simple linear model implemented in ggplot2, while ribbon show the associated 95% confidence interval.*

Appendix V

Duchenne F., Fontaine C., Teulière E. & Thébault E. Phenological traits increase persistence of mutualistic networks and promote positive indirect effects. *In prep.*

Phenological traits increase persistence of mutualistic networks and promote positive indirect effects

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Keywords: phenology | pollination | plant-pollinator | dynamic model | seasonal structure | competition

Abstract

Species traits structuring ecological networks are diverse, such as phenological traits that decouple interaction in time, and morphological traits that mainly create forbidden links. While these differences are likely to affect the indirect effects among species and thus network persistence it remains an overlooked aspect of ecological networks. Here, using dynamic models we focus on how phenological and morphological traits drive community persistence and affect the strength of indirect effect among species. Our results show that within guilds, positive indirect effects are stronger than competition in network structured by phenological traits, thereby increasing network persistence, while this is not the case in networks structured by morphological traits. This buffering of competition by phenological traits allows maintaining specialists, the most vulnerable species, which propagate the most positive effects within guilds and promote nestedness. Our results highlight the effects of phenology as a trait structuring ecological networks in a way promoting coexistence.

Introduction

For a century, biologists have investigated the mechanisms that promote species coexistence in nature, as the pervasive competitive interactions among species are expected to drive species exclusion and limit coexistence (Volterra 1928; Gause 1934). This question becomes even more intriguing when dealing with complex systems, because theoretical works have shown that the stability of a natural community should decrease with the number of species it contains and with the number of interactions among them (Gardner & Ashby 1970; May 1972). Since then, many studies have addressed this historical issue, showing that the structure of ecological networks, i.e. the way interactions among species are organized in ecological communities, enhance species coexistence and the community stability in both food webs (Neutel *et al.* 2002, 2007; Montoya *et al.* 2006; Otto *et al.* 2007) and mutualistic networks (Memmott *et al.* 2007; Okuyama & Holland 2008; Bastolla *et al.* 2009; Thébault & Fontaine 2010).

In mutualistic webs such as plant-pollinator networks, coexistence is likely greatly affected by the relative importance of direct competition and indirect facilitation mediated by the sharing of mutualistic partners between species of the same guild, either plants or pollinators, which depends on network structure. Indeed Bastolla et al. (2009) showed that the nestedness of mutualistic networks increases network persistence by minimizing competition while preserving facilitation. On the other side, Pascual-García & Bastolla (2017) have shown that strong competition within guilds of mutualistic networks decrease their stability. However, even if the role of indirect effects has often been suggested for understanding species coexistence and its links with pollination network structure (Bastolla *et al.* 2009; Thébault & Fontaine 2010), the relative strength of direct and indirect effects remains poorly quantified in mutualistic networks (Gracia-Lázaro *et al.* 2018). Studies on empirical food webs show that indirect effects play a fundamental ecological role (Montoya *et al.* 2009; Salas & Borrett 2011) especially through long indirect paths (Higashi & Nakajima 1995). Two recent studies have started to quantify indirect effects in mutualistic networks and they showed that indirect effects are strongly involved in evolutionary dynamics (Guimarães *et al.* 2017) and network robustness to extinction (Pires *et al.* 2020). These results stress the need to investigate the mechanisms driving the relative importance of direct and indirect effects in mutualistic networks, especially those involved in competition and indirect facilitation, and their consequences for species coexistence.

While network structure, and in particular nestedness, is known to affect competition and facilitation between species in plant-pollinator networks (Bastolla *et al.* 2009), studies have so far ignored the diversity of species traits shaping interactions in these networks. Multiple traits of plants and pollinators are involved in these interactions: flower shape and the length of the feeding apparatus of pollinator (Stang *et al.* 2006; Junker *et al.* 2013), flowering and flying phenology (Junker *et al.* 2013; Gonzalez & Loiselle 2016), floral height (Junker *et al.* 2013), floral scent (Schiestl 2010), etc. Even if all these traits can virtually play a similar structural role by promoting overall network nestedness

(Santamaría & Rodríguez-Gironés 2007; Encinas-Viso *et al.* 2012; Junker *et al.* 2013), they do not structure interactions with the same mechanisms, potentially affecting the relative importance of competition and indirect facilitation between species. While some species traits, such as morphological traits, decrease competition by defining forbidden interactions among species with different traits, other kinds of species traits, such as phenological traits or floral height, decrease competition by decoupling interactions in time or in space. In the case of interactions driven by morphological traits, the absence of competition between two pollinators (or between two plants) is expected to be coupled with the absence of indirect facilitation between these pollinators (or plants) because the species involved are not sharing anymore mutualistic partners (Fig. 1). In contrast, when interactions are structured by phenological traits, the absence of competition between two pollinators does not necessarily imply the absence of facilitation between the two pollinators, as they can still share the same mutualistic partners but at different times (Fig. 1). Thus, from the schematic example presented in Figure 1, we expect that a network mainly structured by phenological traits buffers competition but maintains positive indirect effects within plant and pollinator guilds, thereby promoting greater species persistence than a network mainly structured by morphological traits.

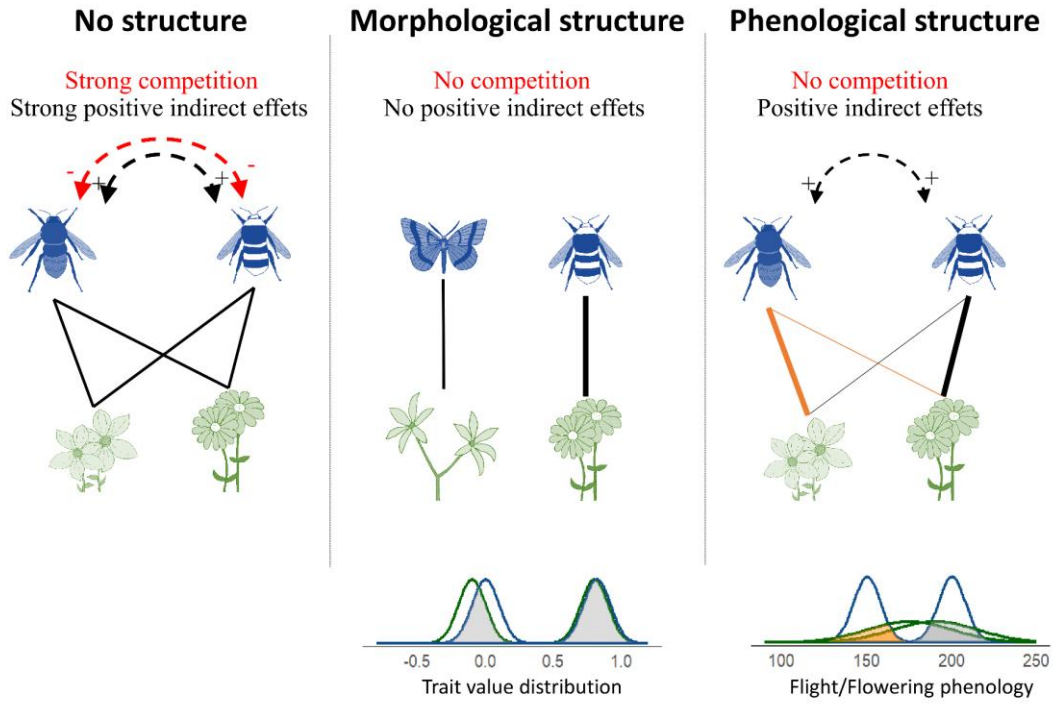

***Fig. 1**: a small pollination network without any structure (left), structured by a morphological trait (middle) or by a phenological trait (right) to remove competition. Links represent mutualistic interactions (+/+) whereas indirect effects among pollinator are represented by dashed arrows. Gaussians represent the trait value distribution or the flowering/flight period for plants (green) and pollinators (blue), and the overlap among them (colored area) representing the interaction strength.*

To investigate how phenological and morphological traits affect the relative contribution of competition and indirect facilitation within guilds in mutualistic networks as well as the network persistence, we developed a dynamic model of pollination networks including intra-guild competition

for access to mutualistic partners. As indirect effects not only encompass effects through paths of length 2 (i.e. indirect effects between species sharing the same interaction partners, e.g. Figure 1), but also all effects through longer paths, quantified the overall direct and indirect effects between species requires to integrate indirect effects overall possible paths. To do so, we quantified the indirect effects at equilibrium using the method of Nakajima & Higashi (1995). Our results reveal that niche partitioning due to the phenological and morphological traits, henceforth phenological and morphological forcings respectively, strongly differ in their consequences on pollination network structure and persistence when there is intra-guild competition.

Methods

We developed an ecological dynamic model describing the interactions between two guilds, pollinators (P) and flowers (F). Species belonging to the same guild compete with each other for partners and species from distinct guilds interact mutualistically. Mutualistic interactions are obligates and defined by both phenological and morphological matching between plants and pollinators.

Phenological and morphological traits structure the networks

Flowering and flight periods, henceforth phenologies, were represented by Gaussians. For both, the mean flowering and flight date (i.e. the mean of the Gaussian) were sampled in from $N(190,70)$, in Julian days, representing the pollination season. Each phenology has a duration represented by the standard deviation of the Gaussian that was sampled from a uniform law between 5 and 40 days, $U(5,45)$. We used circular wrapped Gaussians in order to take into account that the species at the end of the year can interact with species at the beginning of the year and conversely. Traits were defined with the same principle, using a one-dimension niche represented as a Gaussian with a mean sampled from $U(-1.5,1.5)$. The standard deviation of the Gaussian, the width of the trait niche, was sampled from a $U(0.1,0.9)$. Higher the standard deviation is more generalist the species is. Thus, each species was characterized by a phenology and a trait niche, both modeled by Gaussian curves.

Then, we assessed the phenological match and the morphological match among species by calculating the overlapping area of their respective Gaussians. After that, we had two matrixes of same dimensions, one containing phenological matches (P) and one containing the morphological matches (M). In order to modulate the forcings imposed by phenological and morphological traits, we elevated the terms of the matrixes to a given power ranging from 0 to 1. Exponents were called PS and MS for phenologies and morphologies respectively. Higher the exponent is stronger the forcing is. Finally, the interaction matrix (i.e. the backbone of the network), called I below, was built by doing the term product of the two matrices:

$$I = P^{PS} \times M^{MS} \quad (1)$$

I_{ij} represents the interaction strength among the plant i and the pollinator j.

Dynamic model

We model an interaction network, with n_f plant species and n_p pollinator species. *I*, the interaction matrix defined before is of dimension n_f, n_p . The abundance of each pollinator P_j follows this dynamic equation:

$$\frac{dP_j}{dt} = P_j\left(-\frac{P_j}{K_j} - m_j + \frac{\alpha_j \sum_{k=1}^{nf} I_{kj} \times F_k}{1+\beta \sum_{k=1}^{nf} I_{kj} \times F_k + c\sum_{k=1}^{np} \omega_{kj} \times P_k}\right) \quad (2)$$

Where K_j is the carrying capacity of the pollinator *j*, m_j its mortality rate, α_j, β and *c* its functional response parameters. Here, the benefits of mutualism on plant and pollinator species growth were represented by a functional response which saturates with the density of the mutualistic partners (through the handling time parameter β) and decrease with the density of competitors (through the interference term c). In contrast to α, β and *c* were the same for all plant and pollinator species. I_{kj} is the interaction term, from 0 to 1, between the pollinator *j* and the plant *k*. Finally, ω is a matrix of dimensions $n_p \times n_p$, containing intra and inter-specific competition terms among pollinators:

$$\omega_{kj} = \frac{1}{\sum_{i=1}^{nf} I_{ij} \times F_i} \times M_{kj} \times \sum_{i=1}^{nf} F_i \times I_{ik} \times I_{ij}) \quad (3)$$

Where M_{jk} is the intra-guild phenological match between the focal pollinator *j* and the pollinator *k*. By symmetry, the dynamic of the flower of the plant species *i* was described as follow:

$$\frac{dF_i}{dt} = F_i\left(-\frac{F_i}{K_i} - m_i + \frac{\alpha_i \sum_{k=1}^{np} I_{ik} \times P_k}{1+\beta_i \sum_{k=1}^{np} I_{ik} \times P_k + c\sum_{k=1}^{nf} \theta_{ki} \times F_k}\right) \quad (4)$$

Where θ is analog to the matrix ω.

Simulations

We solved the equations numerically using the *lsoda* solver implemented in the R package *deSolve* (Soetaert *et al.* 2010). We stopped the simulation when the maximum of the variance of species abundance on the last 10 time steps was lower than 10^{-9}, which was enough to reach the equilibrium. We simulated 1000 initial random networks. For each of these networks we performed simulations with five distinct values of *MS*, five distinct values of *PS* and with four distinct values of intra-guild competition strength (*c*), leading to a total of 100 000 simulations (1000×5×5×4).

Parameters values used for these simulations are described in the Table 1. All phenological, traits and functional response parameters exhibit inter-specific heterogeneity, except for handling times (β). We did not implement variation on this parameter of functional response to save computing time, as systems reached the equilibrium much faster when species functional responses differed only on the α parameter.

***Table 1:* value of parameters of the dynamic model and phenological and trait values.** *Parameter combinations corresponds to the different combination of intra-guild competition, morphological forcing and phenological forcing, which are the parameter of interest here. Other important parameters vary among the 1,000 initial networks in order to explore a wide set of possible pollination networks.*

Parameter abbreviation	Meaning	Value	Variation among		
			species	1000 initial networks	Parameter combinations
n_f	Initial number of plant species	75	-	No	No
n_p	Initial number of pollinator species	75	-	No	No
K_i	Flower carrying capacity	~ U(10,600)	Yes	Yes	No
K_j	Pollinator carrying capacity	~ U(1,60)	Yes	Yes	No
m_i	Flower mortality rate	~ U(0.2,0.4)	Yes	Yes	No
m_j	Pollinator mortality rate	~ U(0.8,1)	Yes	Yes	No
α_i	Flower pollen release rate	~ U(0.8,1)	Yes	Yes	No
α_j	Pollinator search rate	~ U(0.8,1)	Yes	Yes	No
β_i	Flower saturation term (handling time)	0.9	No	No	No
β_j	Pollinator saturation term (handling time)	0.9	No	No	No
c	Intra-guild competition strength	0/0.25/0.5/0.75	No	No	Yes
MFD_i	Mean Flowering date	~ N (190,70)	Yes	Yes	No
MFD_j	Mean Flight date	~ N (190,70)	Yes	Yes	No
SD_i	Flowering period duration (standard deviation)	~ U(5,40)	Yes	Yes	No
SD_j	Flight period duration (standard deviation)	~ U(5,40)	Yes	Yes	No
TM_i	Plant morphological niche centroid	~ U(-1.5,1.5)	Yes	Yes	No
TM_j	Pollinator morphological niche centroid	~ U(-1.5,1.5)	Yes	Yes	No
G_i	Width of plant morphological niche (standard deviation)	~ U(0.1,0.9)	Yes	Yes	No
G_j	Width of pollinator morphological niche (standard deviation)	~ U(0.1,0.9)	Yes	Yes	No
MS	Morphological trait forcing	0/0.25/0.5/0.75 /1	-	No	Yes
PS	Phenological trait forcing	0/0.25/0.5/0.75 /1	-	No	Yes

Network indices

We quantified 3 indices at the network level: the network viability, which is the proportion of network containing at least one plant and one pollinator; the network persistence, which is the percentage of species with a positive abundance at equilibrium; the nestedness of the interaction matrix, which is the weighted NODF (Galeano *et al.* 2009) of the interaction matrix at equilibrium, after we removed extinct species and rounded the interaction terms I to the 5^{th} digit to avoid numerical issues.

Direct, indirect and total effects partitioning

In order to study how the phenological and the morphological structures affect the propagations of indirect effects we calculated direct effects, indirect effects and the sum of both, the total effects among each pair of species. To do that we used analytic formulas demonstrated by Nakajima & Higashi (1995). As we were not interested in the equilibrium displacement following a perturbation but by estimating the strength of links among species at equilibrium, we used an abundance to inflow perturbation (Nakajima & Higashi 1995), which characterizes the net effect of a sustained unit increase in species j

on species *i* growth rate. Such method allows estimating how a species is affected by an increase of the abundance of another species at equilibrium. In this case, the jacobian matrix (*A*) represents the direct effects among pairs of species (Nakajima & Higashi 1995). Here, as the competition was implemented in a direct way in equations (2) and (4), it was considered as a direct effect. Total effects were estimated from the sensitivity matrix (S), which is the invert of the jacobian matrix:

$$S = A^{-1} \tag{5}$$

Then, the total effect of a species *j* on a species *i* (T_{ij}) was calculated from the coefficients of *S* using the following formula:

$$T_{ij} = \frac{s_{ij}}{s_{ii}s_{jj} - s_{ij}s_{ji}} \tag{6}$$

Thus, the total effect calculated here, was the effect of the disturbed species *j*, on the focus species *i*, by all the paths, excepting paths that revisit one of the both species. By doing that, we removed paths looping on the disturbed or on the focus species, allowing to focus on interspecific relationships. Then, the effect of the species *j* on the species *i* throughout indirect effects (IE_{ij}), was calculated as:

$$IE_{ij} = T_{ij} - A_{ij} \tag{7}$$

Analysis of the indirect effect contributions

We calculated the contributions of indirect effects within ($\overline{IEC_p}$ and $\overline{IEC_f}$) and among ($\overline{IEC_{pf}}$ and $\overline{IEC_{fp}}$) to the total affects received by species, averaged over species pairs. For the contributions among pollinators using the following formula:

$$\overline{IEC_p} = \frac{1}{n_p^2 - n_p}\left(\sum_{j=1}^{n_p}\sum_{i=1\ (i\neq j)}^{n_p}\frac{IE_{ji}}{|IE_{ji}|+|A_{ji}|}\right) \tag{8}$$

The calculation of the contribution among plants $\overline{IEC_f}$ was done by using a formula equivalent to equation (8). The contribution of indirect effects received by plants from pollinators ($\overline{IEC_{pf}}$) was calculated as follow:

$$\overline{IEC_{pf}} = \frac{1}{n_p \times n_f}\left(\sum_{j=1}^{n_p}\sum_{i=n_p+1}^{n_{p+n_f}}\frac{IE_{ji}}{|IE_{ji}|+|A_{ji}|}\right) \tag{9}$$

The calculation of $\overline{IEC_{fp}}$ was done by using a formula equivalent than equation (9). As pollinator persistence is more constrained by intra-guild competition than plant persistence in our case, we focused mostly on pollinators here. To disentangle persistence or nestedness mediated effects and direct effects of phenological and morphological forcings on indirect effect contribution to total effect among pollinator species ($\overline{IEC_p}$), we performed a path-analysis using Structural Equation Modeling (SEM) as it has already done on such model outputs (Thébault & Fontaine 2010). We tested all linear relationships presented in the Figure 4, using a multigroup approach as implemented in the R package *PiecewiseSEM* (Lefcheck 2016). We excluded $c = 0$ as it did not exhibit any variation in intra-guild indirect effect

contributions, because there was no direct link among species from the same guild and thus the indirect effects were equal to the total effects. We used linear mixed-effect models with a random network effect implemented in the R package *nlme* (Pinheiro *et al.* 2020) to account for the fact that the 100 parameter combinations were run on a set of 1000 initial networks. Finally, we showed standardized parameters, the overall effect of a variable on another one being the sum of the paths joining the two variables. We also performed the same analysis on direct and indirect effect strengths, averaged over pollinators, instead of using the contribution of indirect effects to total effects.

Indirect, direct and total effects at the species level

To know the amount of direct, indirect and total effects propagated by each species we summed all the effect of the species *j* to every other species from the same guild, obtaining an effect of the species *j* on the total abundance of plant/pollinators, depending on the guild. To calculate the amount of direct effect propagated by a species *j* to all the species belonging to the same guild (PDE_j), we used the jacobian matrix and the following formula for pollinators:

$$PDE_{j(p)} = \sum_{i=1\ (i\neq j)}^{n_p} A_{ij} \quad (10)$$

We did the same thing for plants and for indirect and total effects, using IE_{ij} and T_{ij} terms respectively instead of A_{ij}. We thus obtained six values: propagated direct, indirect and total effects for plants and pollinators.

Analysis at the species level

First, we assessed how phenological and morphological traits affect the effects received and propagated by species. To place species on the specialist-generalist gradient, we calculated the initial degree and the degree at equilibrium corresponding to the amount of interactions at the initial conditions and at equilibrium, respectively. To do that, for each species we averaged all values belonging to its corresponding column, for pollinators, or row, for plants, of the interaction matrix I, containing interactions strengths. We did that with the initial interaction matrix to calculate the initial degree, and with the final interaction matrix, after removing extinct species, to calculate the degree at equilibrium.

Second, we assessed how phenological and morphological traits affect the species persistence. We grouped the species by the competition coefficient of the simulation and by bins of 0.1 of the species initial degree. The binary persistence variable, equal to one when the species is persistent and to zero when it is extinct, giving the persistence probability once averaged by group. We then plotted the relationship between the persistence probability and the initial degree, using either simulation with a phenological forcing only ($MS = 0$ & $PS > 0$) either a morphological forcing only ($MS > 0$ & $PS = 0$). In the same way, we studied the relationships between average degree at equilibrium and the amount of effect going through species.

Results

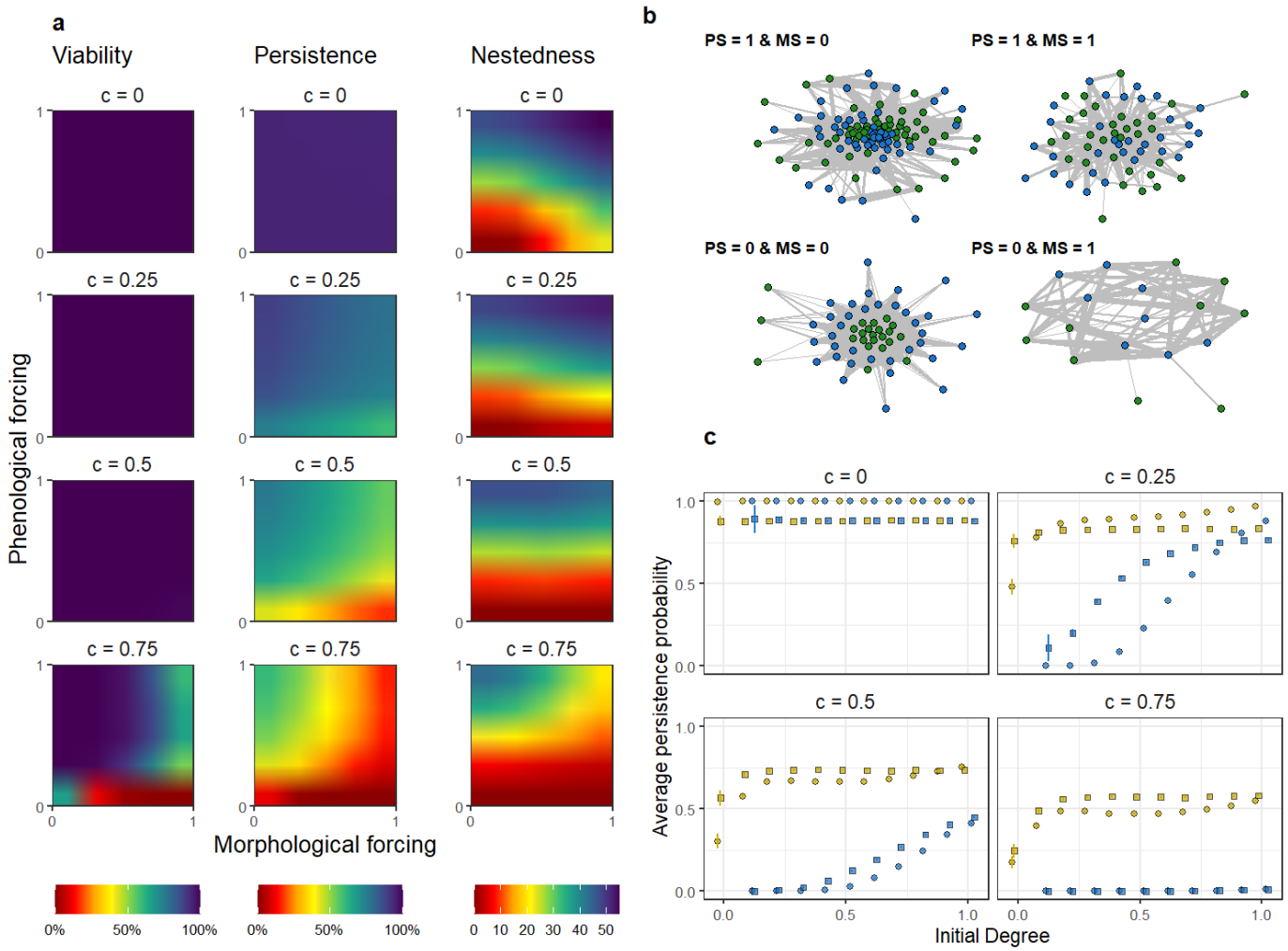

Figure 2: ***network properties at the ecological equilibrium and species persistence****. (a) Network indexes at equilibrium in function of the competition strength, phenological and morphological forcings (PS and MS respectively). Viability is the percentage of final networks with at least one plant and one pollinator, persistence is percentage of surviving species, and nestedness is the weighted NODF of the interaction matrix. (b) Example of networks at equilibrium for extreme values of phenological forcing (PS) and morphological forcing (MS) and for c=0.5. Network was constructed by multiplying interaction values by the geometric mean of associated species abundances. Then we simplified the network by removing link with a weight lower than one. Blue points represent pollinators while green points represent plants. (c) Pollinators (squares) and plant (circles) persistence probability in function of the initial degree. Blue points correspond to simulations with a morphological trait forcing only (PS=0 & MS>0) and yellow points correspond to simulations with a phenological forcing only (PS>0 & MS=0).*

Our results show that the effects of phenological and morphological forcings on network viability, persistence and nestedness are the same in the absence of intra-guild competition ($c = 0$) but they strongly differ when there is intra-guild competition ($c > 0$, Fig. 2a). In absence of intra-guild competition, both phenological and morphological forcings strongly increase network nestedness while they slightly decrease network persistence. Such decrease in persistence is explained by the extinction of species with marginal trait values, which have not enough mutualistic interactions to persist. When intra-guild competition is present, stronger phenological forcing (high *PS* values) leads to higher

network viability, persistence and nestedness (Fig. 2a,b), while stronger morphological forcing (*MS*) decreases network viability and persistence, and fails to promote nestedness (Fig. 2a,b). Differences in nestedness between the cases with and without intra-guild competition are due to species extinctions as nestedness is measured on the interaction matrix directly without accounting for species abundances. As expected, higher intra-guild competition decreases network viability and persistence but our results reveal that such effects are dampened when phenological forcing is strong (Fig. 2a).

Differences in network persistence and nestedness between the two types of forcings can be understood further by considering species persistence as a function of species initial degree in the networks. When there is intra-guild competition, specialist species, that is to say species with short flight period and/or a narrow morphological trait niche, have a lower persistence probability than generalist species (Fig. 2c & S1). The lower persistence of specialist species compared to generalists is attenuated when networks are structured by a phenological trait compared to when they are structured by a morphological trait (Fig. 2c). By maintaining specialist species at equilibrium, the phenological forcing thus maintains the heterogeneity in the degree distribution required to get a nested network (Bascompte *et al.* 2003). Indeed, nestedness is negatively correlated to the average degree of persistent species (Fig. S2). This explains why networks with phenological forcing retain high nestedness compared to networks with morphological forcing.

As expected, the presence of intra-guild competition strongly affects the average strength of direct and indirect effects between species in the networks at equilibrium (Figure 3a,b). When there is no intra-guild competition, implemented here as a direct effect within guilds, positive indirect effects are the only contributors to the total positive effects within guilds, for both plants and pollinators. In that case, indirect effects among guilds are also positive, but their contributions to total positive effects among species are very weak (Fig. 3b). When intra-guild competition is present ($c > 0$), the total effects among species from the same guild tend to become negative on average. This is due to direct competition between species, as indirect effects within guilds remain positive, probably because species from the same guild often maintain common partners in addition to competing for resources. However, indirect effects among guilds become on average negative when $c > 0$, because any species having several mutualistic partners tend to promote competition among these partners (Fig. 3b). In this case, indirect effects contribute about to the half of the total effects among species within guilds and slightly less among guilds (Fig. 3b). Thus, since indirect effects can be strong enough to balance the competition within guilds and mutualistic interaction among guilds, they can in some cases lead to negative total effects among plants and pollinators or positive total effects among species from the same guild (Fig. 3c). Consistently with what we expected, when intra-guild competition is present, total effects within guilds are les negative when there is phenological forcing than when morphological forcing is present (Fig. S3). However, there are strong differences in species diversity and network nestedness at equilibrium between the two types of forcing (Fig. 2), which could mediate such effect. To disentangle

the contribution of diversity and nestedness from the effects directly due to the phenological and morphological forcings, we used a path-analysis. We focused on the contribution of indirect effects to total effect among pollinators, as total effects on pollinators are significantly affected by changes in other pollinator abundances (within guild total effects) while total effects on plants are mostly mediated by among guild effects.

The path analyses first reveal that diversity at equilibrium strongly decreases the contribution of positive indirect effects to total effects among pollinators, while this contribution is slightly increased by nestedness (Fig. 4). Second, independently from the effects mediated by diversity and nestedness, phenological forcing increases the contribution of positive indirect effects to total effects among species from the same guild (Fig. 4). In contrast, morphological forcing strongly decreases the contribution of positive indirect effects among pollinators (Fig. 4). Further, the interaction between the phenological and the morphological forcings (*PS* and *MS*) has a strong negative effect on the contribution of positive indirect effects to total effect among pollinators, suggesting that combining the forcings decrease the contribution of positive indirect effects among pollinators (Fig. 4). Those results mean that, in contrast to morphological traits, phenological traits, which decouples interaction in time, favors a less negative balance between indirect effects and competition among pollinators, buffering much more competition.

Importantly, phenological and morphological forcings affect the balance between competition and positive indirect effects among pollinators in two different ways: while phenological forcing increase positive indirect effects among pollinators but also competition, morphological forcing do the opposite, decreasing competition but also positive indirect effects (Fig. S4). Thus, the positive effect of phenological forcing on indirect effects contribution is due to the fact that it increases more positive indirect effects than it increases competition, while morphological forcing failed to decrease competition more than it decrease positive indirect effects among pollinators (Fig. S4). The larger contribution of positive indirect effects to total effects within the guild of pollinators when networks are structured by phenological traits might also be linked to the greater persistence of specialists in such networks (Fig. 2c). Indeed, by estimating the amount of effects propagated by species (i.e. the effect of a species on the summed abundances of other species from the same guild), we show that specialist species tend to propagate less negative total effects within guilds than generalists (Fig. 4b). Although generalist species propagate stronger direct and indirect effects (Fig. S6), as they have many mutualistic partners and thus many competitors, specialists tend to propagate more positive indirect effects relatively to their direct competitive effects (Fig. S6). We detect the same patterns as in Fig. 4 for the contribution of positive indirect effects to total effects among plants, but only for strong intra-guild competition strength (Fig. S5). This difference between plants and pollinators might be related to the weaker importance of within-guild effects for plants than for pollinators (Fig. 3a).

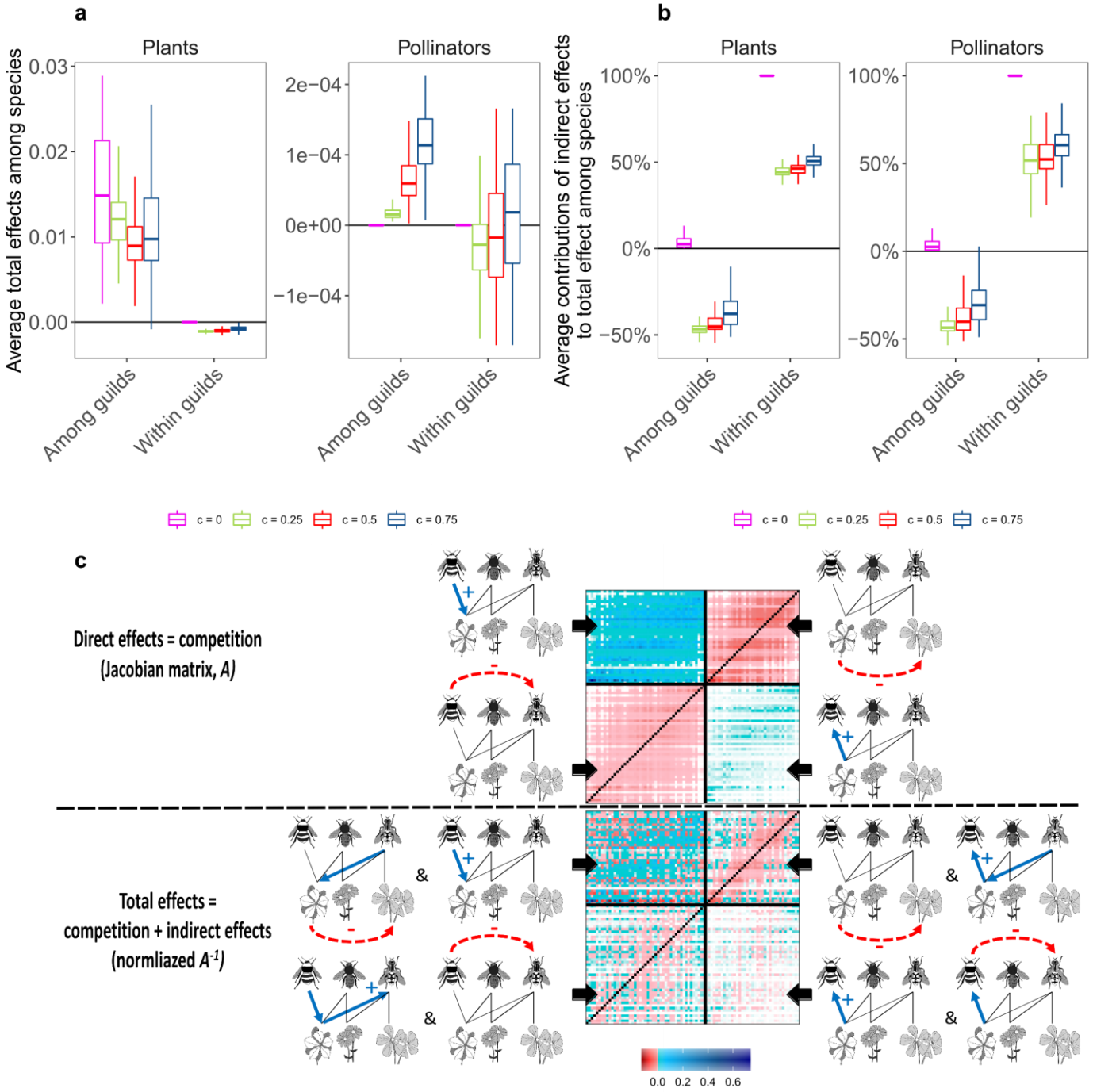

Figure 3: ***Within and among guilds effect partitioning at equilibrium and their relative contributions to total effects***. *(a) Jacobian matrix (A, high) and the total effect matrix (corresponding to the normalized A^{-1}, low) of a network at equilibrium, for MS=0.5, PS=0.5 and c=0.5. Matrix diagonals was uncolored to focus on inter-specific relationships (see Methods). In the Jacobian matrix blocks along the diagonal represent the competition effects while off-diagonal blocks represent plant-poll direct effects. The total effect matrix represents the sum of the direct and indirect effects among species, so the term to term difference between both matrixes give the indirect effects only. Schemes represent examples of short path through an effect received by a pollinator/plant occurs but in our method we integrated indirect effects over all possible paths. Here within guilds direct effects correspond to competition for mutualistic partners, as it was implemented as a direct effect in the model (see Methods). (b) Within and among guilds strength of total effects received by species averaged at the guild level for plant and pollinators in function of the competition strength. (c) Within and among guilds contributions of indirect effects (in %) to total effects averaged at the guild level, received by plants and by pollinators in function of the competition strength. In (b) and (c) outliers points are not represented to preserve readability.*

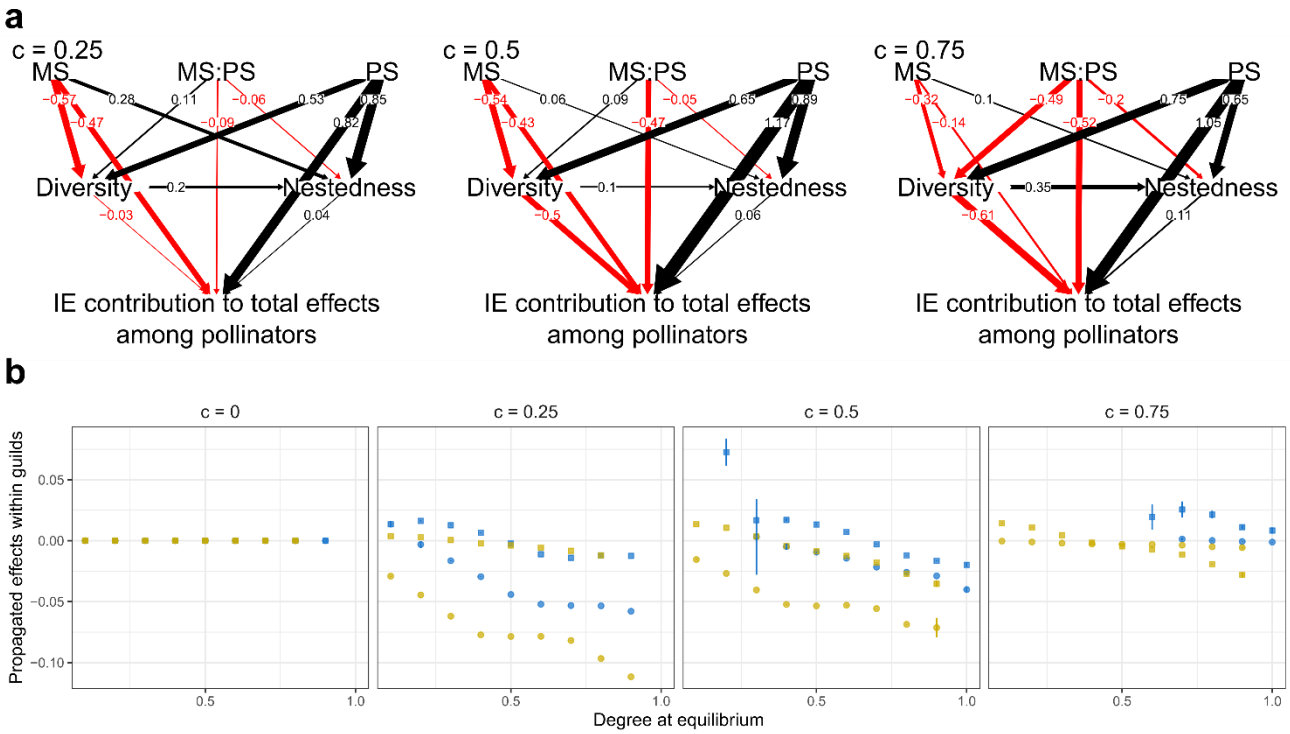

Figure 4: ***relationships among traits, structure, diversity and contribution of indirect effects to total effects among pollinators and propagated effects within guilds by species****. (a) Values on arrows are standardized coefficients of the multi-group path-analysis performed on data for distinctive intra-guild competition strength (c). This model includes an interaction (MS:PS) between the phenological (PS) and morphological (MS) forcings. Diversity is the number of persistent species at equilibrium. (b) Total effects propagated by pollinators (squares) and by plant (circles), at equilibrium, in function of the species degree at equilibrium. Blue points correspond to simulations with a morphological trait forcing only (PS=0 & MS>0) and yellow points correspond to simulations with a phenological forcing only (PS>0 & MS=0). Error bars are 95% confidence interval. Values are averaged by tenths and points are slightly staggered for readability.*

Discussion

Our results show that phenological forcing of plant-pollinator interactions dampens the negative effects of competition for mutualistic partners on species persistence, leading to greater diversity and network nestedness than when interactions are structured by morphological traits. As hypothesized, we find that these two mechanisms affect indirect effects in two very distinct ways: while morphological forcing decreases both competition and positive indirect effects among species form the same guilds, phenological forcing increases competition and positive indirect effects among species form the same guilds. Most importantly, once network differences in nestedness and diversity are accounted for, we show that phenological forcing leads to a less negative, or more positive, balance between competition and positive indirect effects within guilds at equilibrium. Since indirect effect estimation is based on a linear approximation around the equilibrium state, we cannot estimate indirect effects during the

transient dynamic leading to the equilibrium, which prevents to properly assess if they are a cause or a consequence of network persistence. However, there is no difference between networks with a phenological forcing and networks with a morphological forcing when intra-guild competition is null. This suggests that the positive effect of phenological forcing on persistence results from changes in net effects of competition and facilitation between species from the same guild, in which indirect effects contribute for about 50%. Taken together, our results show that the types of species traits shaping interactions in mutualistic networks affect species coexistence, by altering the balance between competition and indirect facilitation among species from the same guild.

Recent studies have highlighted the importance of phenology for structuring pollination networks. Several studies have showed that phenology was a major predictor of plant-pollinator interactions by analyzing the temporal dynamics of networks (Gonzalez & Loiselle 2016; CaraDonna *et al.* 2017; Manincor *et al.* 2020). By performing a meta-analysis on 24 plant-hummingbird networks, Sonne *et al.* 2020 also showed that both morphological matching and phenology overlap strongly explained interaction frequencies in networks, with a varying importance of these two mechanisms along latitude. Our results thus suggest that such important phenological forcing is key to the maintenance of diversity in plant-pollinator natural communities. In addition, our findings on the consequences of phenological forcing can be generalized to other traits than phenology. Indeed, any other trait decoupling interactions in time or space, as for example traits associated with daytime activity and flower opening or with flight and flower heights, should similarly maintain indirect facilitation within guilds and promote species coexistence. For instance, differences in flight and flower heights could allow two pollinator species that fly at different height to avoid competition whilst still interacting with the same plant population, or even with the same individual plant if the plant has flowers at different heights (e.g. flowering trees). As pollinators have been shown to differ in flower visitation at small spatial and temporal scales (Albrecht *et al.* 2012; Baldock *et al.* 2015; Knop *et al.* 2017), we expect that the mechanisms highlighted in this study are widespread in pollination networks.

As expected from previous studies (Bastolla *et al.* 2009), we show that competition is a major driver of the persistence of plant-pollinator networks and that the differential effects of phenological and morphological traits depend on the presence of competition. Empirical studies show that competition between plants and between pollinators for access to mutualistic partners can be strong in pollination networks (Pleasants 1980; Campbell 1985; Henry & Rodet 2018). Our modeled scenario with no competition should thus be seen as a null expectation or a control. While competition is known as an important evolutionary and ecological driver of plant-pollinator evolution (Levin & Anderson 1970; Jones *et al.* 2012; Maeng *et al.* 2012), indirect effects occurring through long path have been recently shown as important driver of evolutionary (Guimarães *et al.* 2017) and ecological (Pires *et al.* 2020) dynamics in mutualistic networks.

Seasonal structure of ecological communities was known to increase diversity of ecological networks by decreasing competition (Encinas-Viso *et al.* 2012; Rudolf 2019). Here we show that in addition to competition, positive indirect effects among species from the same guild (i.e. facilitation) play an important role in maintaining diversity in a competition context with phenological forcing. We did not focus only on indirect-effects among species sharing mutualistic partners, but we quantified indirect effects among species from the same guild over all possible paths, which allows encompassing indirect effects including those with long paths. Our results further bring support to the findings of Bastolla et al. (2009) by showing that network nestedness favors a positive balance between competition and positive indirect effects among species from the same guild. While Bastolla et al. (2009) modeled competition independently from the structure of mutualistic interactions, within-guild competition is directly related to the sharing of mutualistic partners in our model. This suggests that nestedness might still favor network persistence even when it is associated with greater potential competition in addition to larger facilitation. We also suggest that the contribution of indirect effects tend to decrease with the diversity of mutualistic networks, a pattern that has been highlighted previously in food webs (Iles & Novak 2016). In food webs, such effect of diversity is related to a skewer distribution of interaction strengths in diverse webs, leading to a greater predictability of the effects of press perturbations when network complexity is higher (Iles & Novak 2016). It is unclear whether the same mechanisms act in mutualistic networks and the relation between network complexity and the influence of indirect effects remain to be fully investigated in that case.

Furthermore, our results also highlight that the persistence of specialist species is key to understand the effects of phenological forcing at equilibrium. As revealed by Saavedra et al. 2011, we found that specialists are the species that promote the most the nestedness of networks at equilibrium, as they create heterogeneity in degree distribution (Bascompte *et al.* 2003), but they are also the most vulnerable species. Including a seasonal structure better protects specialist species from extinction, which provides new insights on mechanisms that could maintain those vulnerable species in networks. Consequently, we find that phenological forcing increase much more the nestedness than morphological forcing, that is expected to increase the resilience and the robustness of the networks to perturbations (Memmott *et al.* 2007; Thébault & Fontaine 2010). Moreover, we find that specialist species propagate more positive indirect effects to other species relatively to their direct competitive effects than generalists have. Thus, in addition to promotes positive indirect effects within guilds by decoupling interaction in time, phenological forcing protects species that have the less negative balance between positive indirect effects and competitive effects, thereby tilting the balance even more towards facilitation rather than competition.

While the role of phenological traits in ecological networks remains poorly investigated theoretically, here we show that it allows to increase network persistence and promote nestedness much more than in networks structured by a morphological trait. Benefits of the phenological traits mainly occur because

they decouple interaction across time, making the balance between facilitation and competition less negative than morphological traits. Such results provide a mechanism explaining why the few pollination networks datasets with seasonal dynamic analyzed so far tend to exhibit a higher phenological than morphological forcing (Gonzalez & Loiselle 2016; CaraDonna *et al.* 2017). Recent studies showed that climate warming is shifting pollinator flight periods and flowering periods leading to changes in the seasonal structure of pollinator or plant assemblages (Diez *et al.* 2012; Theobald *et al.* 2017; Duchenne *et al.* 2020). Such changes are likely to affect competition pressures (Rudolf 2019) as well as positive indirect facilitation in mutualistic assemblages, possibly leading to the extinction of the vulnerable but key species for network persistence.

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Supplementary:

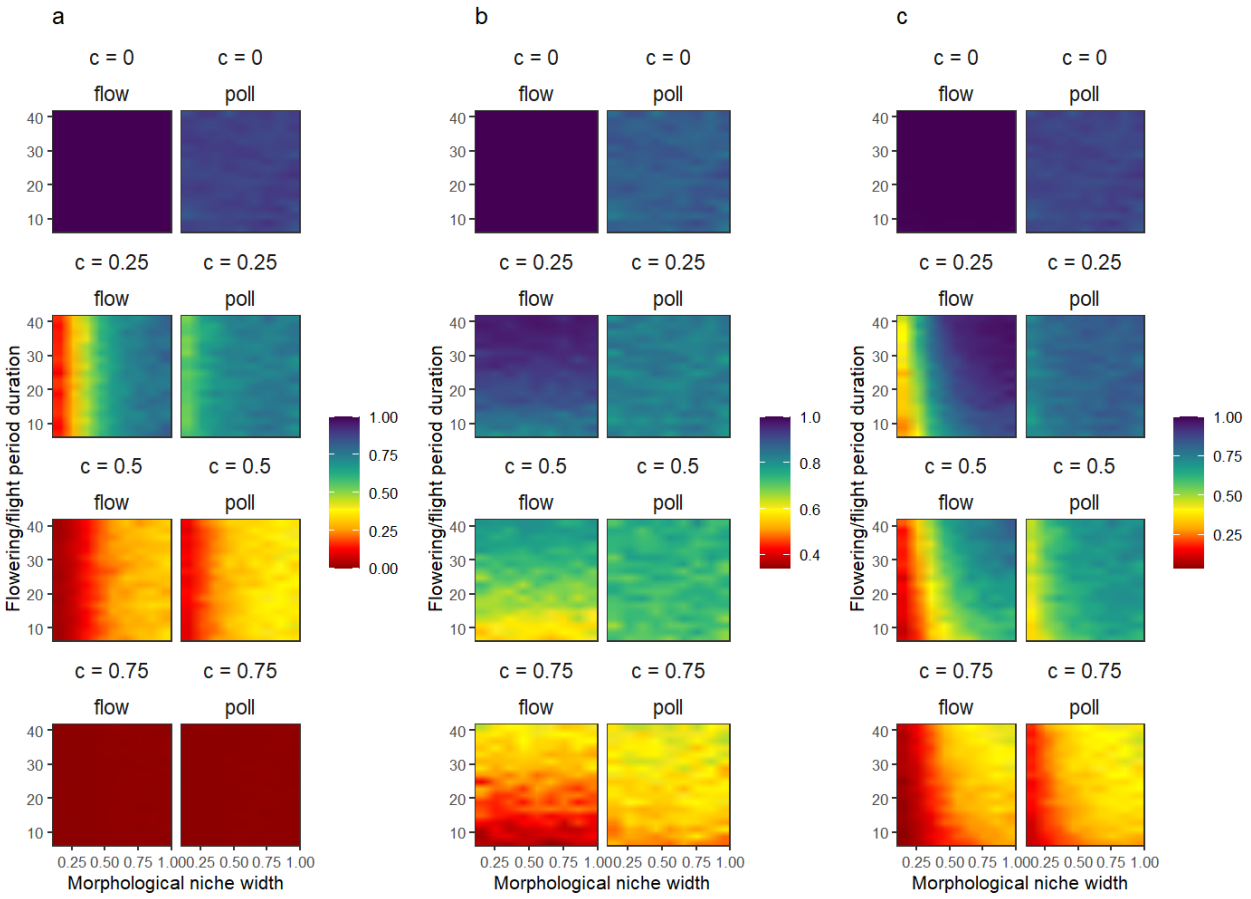


Figure S1: ***Persistence probability in function of the flowering/flight period duration and of the morphological niche width.*** *(a) when there is a morphological forcing only (MS>0 & PS<0), (b) when there is a phenological forcing only (MS=0 & PS>0), (c) when there are both phenological and morphological forcings (MS>0 & PS>0). Values are shown for plants (flow) and pollinators (poll).*

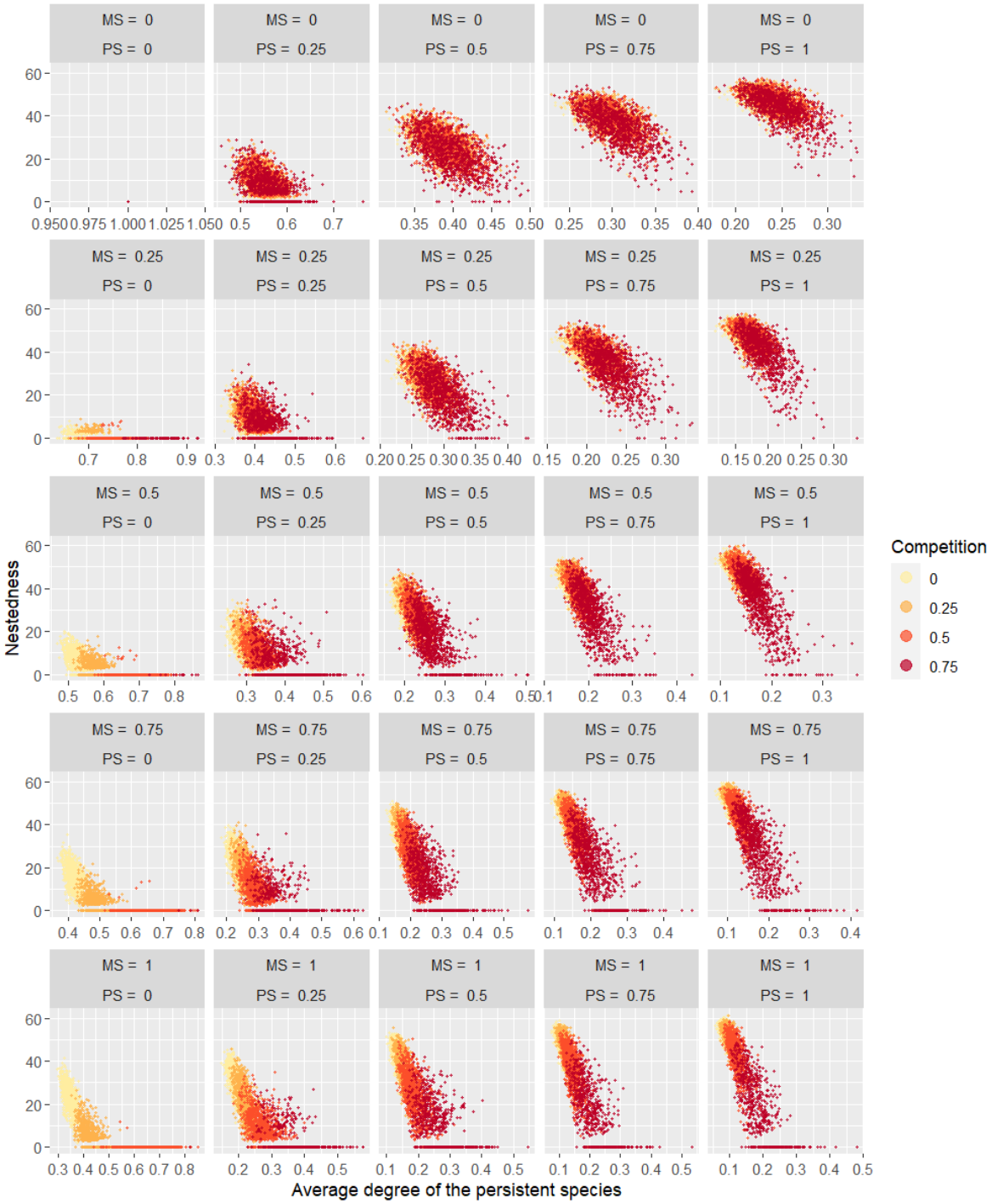


Figure S2: ***Nestedness is linked to the average degree of persistent species at equilibrium.*** *Relationship between the nestedness and the average degree of persistent species at equilibrium, in function of the phenological (PS) and morphological (MS) structure strength, and of the competition strength.*

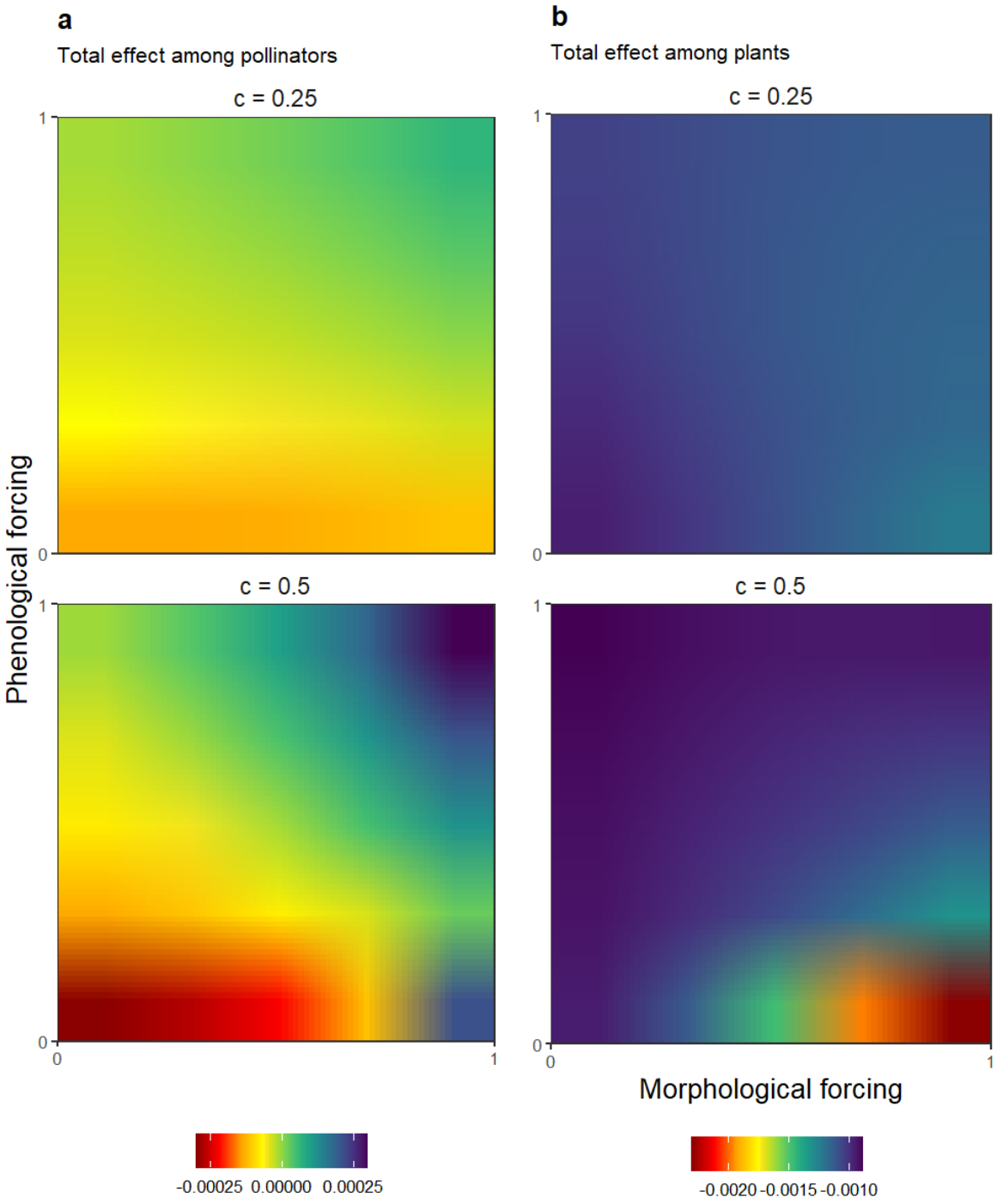
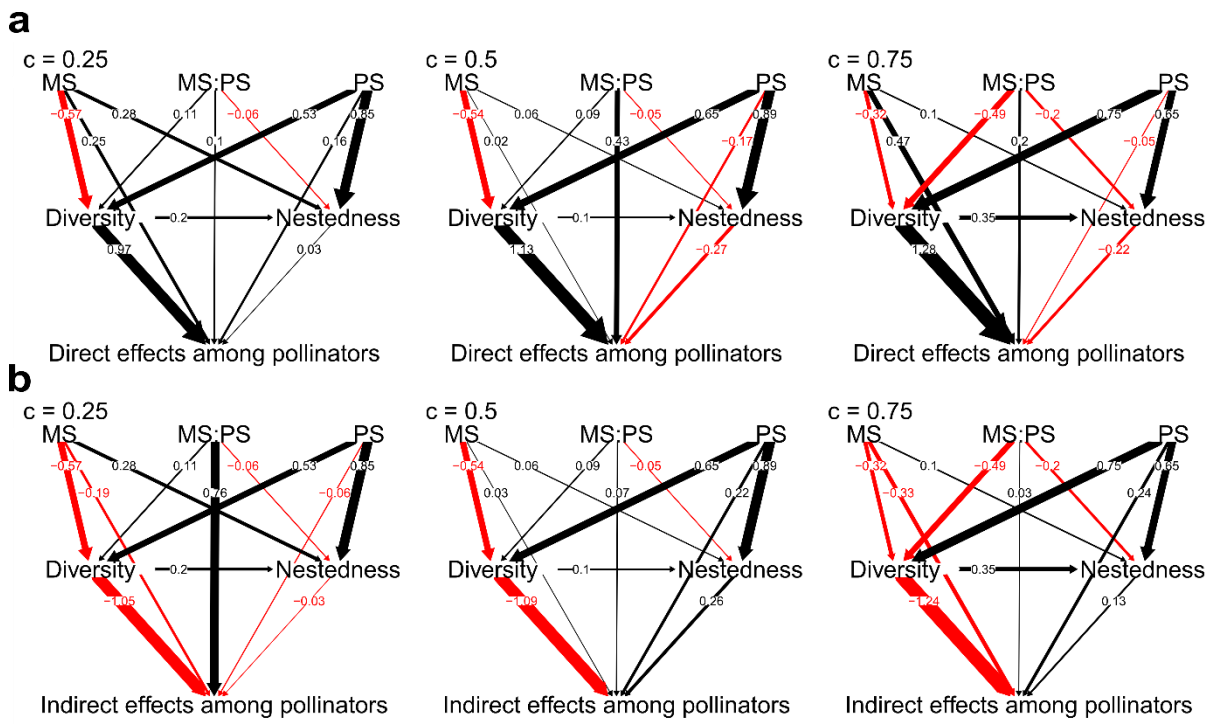
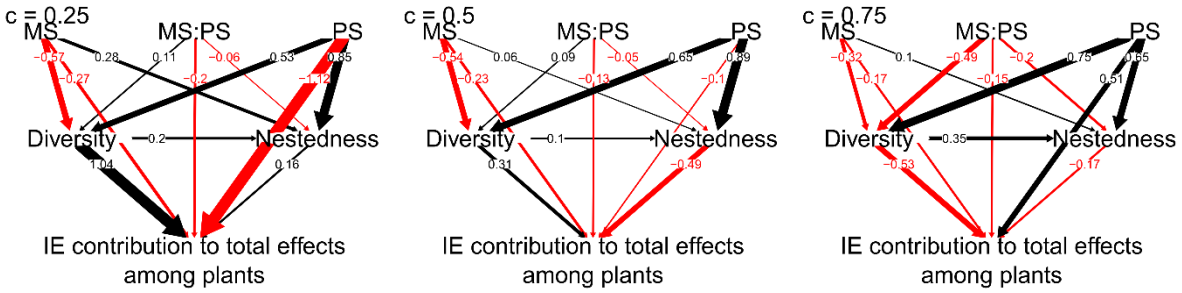


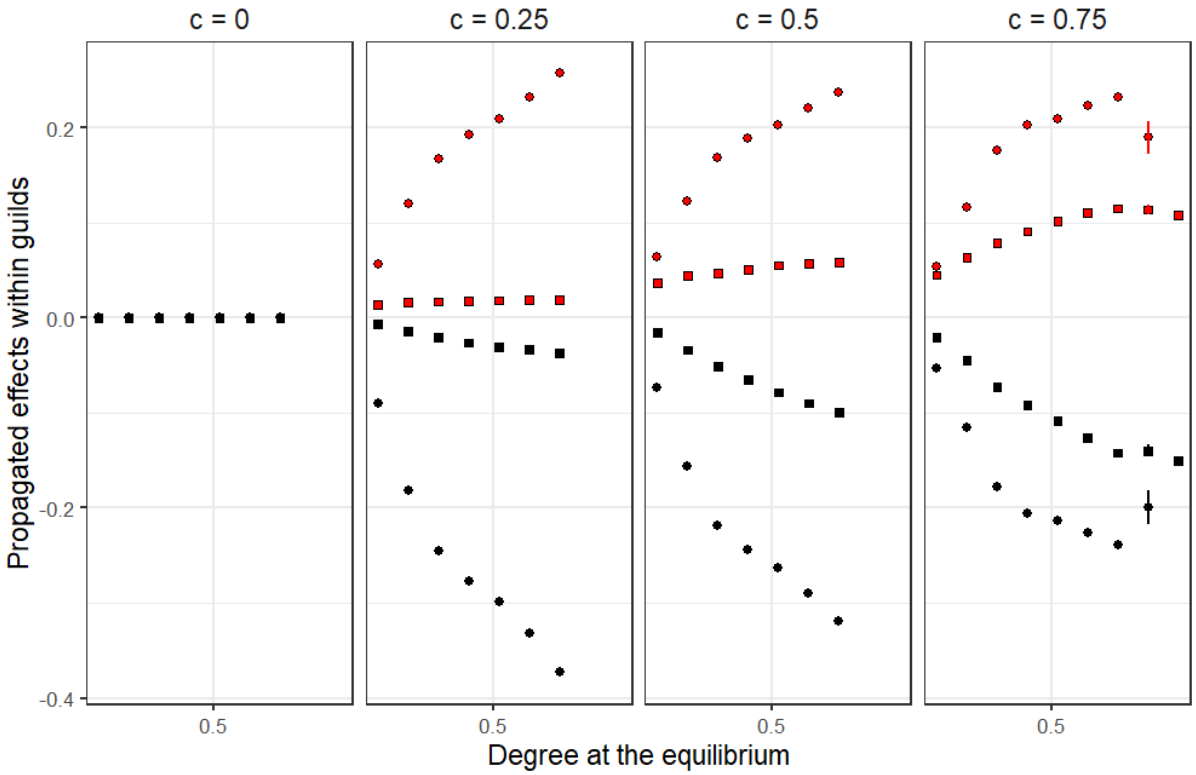
Figure S3: ***Average total effect among species.*** *(a) Among pollinators and (b) among plants for the two intermediate levels of intra-guild competition (c).*



<u>Figure S4:</u> ***Strength of effects among pollinators in function of the diversity, the phenological and morphological structure strengths (PS and MS) and the competition strength (c)***. *(a) Direct (competition) and (b) indirect effects. In (a), as direct effects represent competition among pollinators, which is negative, an increase of direct effects means a decrease of the competition pressure. Values on arrows are standardized coefficients of the multi-group path-analysis performed on data for distinctive intra-guild competition strength. This model includes an interaction (MS:PS) between the phenological (PS) and morphological (MS) structure strengths. Diversity is the number of persistent species at equilibrium and Nestedness if the quantified NODF of the final interaction matrix (see Methods).*



<u>Figure S5:</u> contribution of indirect effects to total effects among plants in function of the diversity, the phenological and morphological structure strengths (PS and MS) and the competition strength (c). *Values on arrows are standardized coefficients of the multi-group path-analysis performed on data for distinctive intra-guild competition strength. This model includes an interaction (MS:PS) between the phenological (PS) and morphological (MS) structure strengths. Diversity is the number of persistent species at equilibrium and Nestedness if the quantified NODF of the final interaction matrix (see Methods).*



<u>Figure S6:</u> ***direct and indirect effects propagated by species in fuction of their degree.*** *Within guilds propagated effects by plant (circles) and pollinator (squares), for indirect (red) and direct (black) effects, averaged over all simulation with a phenological forcing and a morphological forcing (MS > 0 & PS > 0). The degree is the amount of interactions (see Methods), higher it is more generalist the species is. Error bars are 95% confidence interval.*

Appendix VI

Duchenne F., Fontaine C. & Thébault E. The robustness of pollination networks to phenological shifts depends on competition and diversity. *In prep.*

The robustness of pollination networks to phenological shifts depends on competition and diversity

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Abstract

Increasing evidence shows that climate change affects the seasonal timing of biological events, putatively affecting the web of life by leading to temporal mismatches among interacting species. However, understanding the consequences of these phenological shifts for communities remains a challenging and overlooked task. Here we propose to use a dynamic model, including competition and interaction rewiring, to study how shifts in pollinator flight periods and plant flowering periods affect pollination networks. We assessed the consequences of two main dimensions of phenological shifts, varying independently the average mismatch between plants and pollinators as well as the heterogeneity of phenological shifts within guilds. We show that competition decreases the robustness of pollination network to phenological mismatch between plants and pollinators and to heterogeneous phenological shifts, both kinds of phenological shifts equally affecting pollination networks. High diversity and short pollination season buffer the effects of the heterogeneity in phenological shifts but not of the average plant-pollinator mismatch. The decrease of the strength of mutualistic interactions is the main driver of species decline. However, phenological shifts also affect competition pressures which play a non-negligible role in the changes in species abundance despite being often overlooked. Our results highlight a positive diversity-stability relationship, raising concerns that pollinator decline acts synergistically with ongoing phenological shifts, leading to negative consequences on pollination function and services.

Introduction

Climate change is affecting the seasonal timing of many biological events (Parmesan 2006), such as flowering (Fitter & Fitter 2002), breeding (Nussey *et al.* 2005), activity period (Roy & Sparks 2000). Since there is a substantial heterogeneity in the phenological responses to climate change among species (Diez *et al.* 2012) and among trophic levels (Thackeray *et al.* 2016), such changes could lead to a seasonal desynchronization of species interacting directly, such as plants and pollinators (Memmott *et al.* 2007), or indirectly, via the complex web of interacting species (Carter *et al.* 2018; Rudolf 2019). By affecting direct and indirect interactions in ecological communities, phenological shifts in response to climate change are likely affecting ecological function and services.

Pollination is a mutualistic interaction between plants and pollinators, essential to the sexual reproduction of a major part of plants and to the feeding of pollinators, which get floral resources, such as nectar or pollen. It is a key ecosystem function and services that is known to be threatened by a risk of temporal mismatch between the flowering period of plants and the activity period of their pollinators (Memmott *et al.* 2007; Gérard *et al.* 2020). A temporal mismatch between plant flowering and pollinator activity period would thus strongly affect plant and pollinator viability. Such mismatch can be due to a difference in the average strength of shifts between plants and pollinators (Kudo & Cooper 2019) or to a strong heterogeneity hidden behind the average responses (Memmott *et al.* 2007). Indeed, species that interact with more than one partners would not be able to follow each of them if they are not responding with the same strength and direction to climate change, thereby leading to temporal mismatch among mutualistic partners. Phenological mismatches among interacting species, due to differences in the average strength of the phenological shifts or heterogeneity in the latter, are known to negatively affect species persistence but also related ecological functions (Memmott *et al.* 2007; Kudo & Ida 2013). However, while most of the emphasis on this issue has been made on the difference in average phenological response between plants and pollinators, the relative consequences of the heterogeneity in phenological shifts and of the average plant-pollinator mismatch on species persistence remain unclear.

While many empirical and theoretical studies focus on phenological mismatches between interacting species, in a mutualistic (Memmott *et al.* 2007; Rafferty & Ives 2011) or antagonistic (Saino *et al.* 2009; Asch *et al.* 2013; Renner & Zohner 2018) context, indirect interactions are also widely neglected (Rudolf 2019). In mutualistic networks, these indirect effects have been shown to be an important driver of the evolutionary trajectories of species (Guimarães *et al.* 2017) as well as an important determinant of extinction cascades (Pires *et al.* 2020). Since the seasonal structure of plant and pollinator communities is changing due to the effect of phenological responses to climate change (Diez *et al.* 2012; CaraDonna *et al.* 2014; Duchenne *et al.* 2020), those indirect effects are likely to change. Indeed, the seasonal structure of plant and pollinator communities has an important role in plant-pollinator networks (Encinas-Viso *et al.* 2012; Junker *et al.* 2013; Gonzalez & Loiselle 2016; CaraDonna *et al.* 2017), by determining network robustness to perturbations (Ramos–Jiliberto *et al.* 2018). Since this seasonal

structure is inherited from historical eco-evolutionary dynamic processes largely influenced by indirect effects, such as competition (Jones *et al.* 2012; Maeng *et al.* 2012), any modification of the seasonal structure is likely to increase competition pressures and thus lead to changes in species abundances. Competition is known to shape species' responses to climate change over space (Alexander *et al.* 2015) and theoretical models show that it can have the same effect regarding phenological shifts (Rudolf 2019). This suggests that changes in the indirect competitive interactions could be at least as important as the loss of direct interactions for species in the effect of phenological shifts on species. Thus, we expect that phenological shifts can affect species persistence and ecological networks through a modification of direct interactions, but also more perniciously through a modification of the invisible indirect effects such as competition for shared resources.

For instance, interaction rewiring in pollination networks is relatively high (CaraDonna *et al.* 2017) and a high diversity in pollination webs could protect them from temporal mismatch with mutualistic partners (Bartomeus *et al.* 2013) if plant and pollinators are able to change their mutualistic partners. Moreover, mutualistic networks are highly nested, a structure which occurs when specialist species tend to interact with species that interact with more generalist ones (Bascompte *et al.* 2003) and which buffers competition (Bastolla *et al.* 2009). Such nested structure is partly due to the seasonal structure of pollination network (Encinas-Viso *et al.* 2012), and it promotes the robustness of pollination networks to species extinctions (Memmott *et al.* 2004). Any changes in the seasonal structure, because of phenological shifts, could thus affect plant-pollinator robustness by modifying the structure of pollination networks. The structure of mutualistic networks also determines their resilience, measured as the time to return to an equilibrium after a small perturbation (Thébault & Fontaine 2010), and we might expect some relation between resilience and network response to stronger and more persistent perturbations such as phenological shifts.

To our knowledge, two studies focused on the effect of the phenological shifts on pollination networks (Memmott *et al.* 2007; Revilla *et al.* 2015), and they mainly tackled the question by using non-dynamic models (Memmott *et al.* 2007). Moreover, those models mainly focused on the loss of direct mutualistic interactions, without considering competition or any other indirect effects, and not considering interaction rewiring (Memmott *et al.* 2007; Revilla *et al.* 2015). Here, we used a dynamic model, including competition and interaction rewiring, to assess the robustness of pollination networks to two distinctive dimensions of phenological shifts, heterogeneity in phenological shifts and average plant-pollinator mismatch in phenological shifts. We then assessed the mechanisms involved in network robustness and changes in species abundances.

Methods

We developed an ecological dynamic model describing the interactions between two guilds, pollinators (P) and flowers (F). Species belonging to the same guild compete with each other for interacting partners, and species from distinct guilds interact mutualistically.

Dynamic model

We used the model developed by Duchenne et al. (n.d.) modeling a plant-pollinator interaction networks with intra-guild competition for mutualistic partners. Mutualistic interactions are obligate and defined by both phenological and trait matching between plants and pollinators.

Phenological and morphological traits structure the networks

Since pollination networks seem structured mainly by phenological and morphological traits (Junker *et al.* 2013; CaraDonna *et al.* 2017; Manincor *et al.* 2020), we used a two dimensional trait matching, using a phenological trait and a morphological trait. Flowering/flight periods, henceforth phenologies, are represented by Gaussians. For both plants and pollinators, the mean flowering/flight date (i.e. the mean of the Gaussian) is sampled in from $\mathbb{N}(190, \sigma^2_{MFD})$, expressed in Julian days, where 190 is the center of the pollination season and σ^2_{MFD} its length (i.e. duration). Each phenology has a duration represented by the standard deviation of the Gaussian that is sampled from a uniform law between 10 and 45 days, $U(10,45)$. We used circular wrapped Gaussians in order to take into account that the species at the end of the year can interact with species at the beginning of the year and conversely. Traits are defined with the same principle, using a one dimension niche represented as a Gaussian with a mean sampled from $U(-1,1)$. The standard deviation of the Gaussian, defining the width of the trait niche, is sampled from $U(0.1,0.9)$. The standard deviation is higher for more generalist species. Thus, each species is characterized by a phenology and a trait niche, both represented by Gaussian curves.

The strengths of the mutualistic interactions are defined by the phenological overlaps and the morphological overlaps between plants and pollinators. The overlaps are calculated by the integral of the minimum of the Gaussians of each possible pair of pollinator and plant. This gives two matrices with the same dimensions, one containing phenological overlaps and another one containing the morphological overlaps. Finally, the interaction matrix (i.e. the backbone of the network), called I below, is built by doing the term product of the two matrices.

Dynamic model

We model an interaction network with n_f plant species and n_p pollinator species. I, the interaction matrix defined before is of dimension n_f, n_p . The abundance of each pollinator P_j follows this dynamic equation. It is expressed as:

$$\frac{dP_j}{dt} = P_j\left(-\frac{P_j}{K_j} - m_j + \frac{\alpha_j \sum_{k=1}^{n_f} I_{kj} \times F_k}{1 + \beta \sum_{k=1}^{n_f} I_{kj} \times F_k + c\sum_{k=1}^{n_p} \omega_{kj} \times P_k}\right) \quad (1)$$

Where K_j is the carrying capacity of the pollinator *j*, m_j its mortality rate, α_j, β and *c* its functional response parameters. In contrast to α and β, *c* is the same for all plant and pollinator species, and it represents the strength of the competition for partners. I_{kj} is the interaction term, from 0 to 1, between the pollinator *j* and the plant *k*. Finally, ω is a matrix of dimensions $n_p \times n_p$, containing intra and inter-specific competition terms among pollinators:

$$\omega_{kj} = \frac{1}{\sum_{i=1}^{n_f} I_{ij} \times F_i} \times M_{kj} \times \sum_{i=1}^{n_f} F_i \times I_{ik} \times I_{ij}) \quad (2)$$

The intensity of the effect of competition of pollinator k on pollinator j ω_{kj} depends on M_{kj} , which is the intra-guild phenological overlap between the focal pollinator *j* and the pollinator *k*, on the strengths of the interactions of the pollinator *k* on the different plants visited by pollinator *j* as well as on the relative dependence of pollinator *j* on these plants. By symmetry, the dynamic of the flower of the plant species *i* was described as follow:

$$\frac{dF_i}{dt} = F_i\left(-\frac{F_i}{K_i} - m_i + \frac{\alpha_i \sum_{k=1}^{n_p} I_{ik} \times P_k}{1 + \beta \sum_{k=1}^{n_p} I_{ik} \times P_k + c \sum_{k=1}^{n_f} \theta_{ki} \times F_k}\right) \quad (3)$$

Where θ is analog to the matrix ω.

Simulations and phenological shifts

First we solved the equations numerically until the maximum of the variance of species abundance on the last 10 outputs was lower than 10^{-9} (Fig. 1), which corresponds to the first equilibrium. From this point, we shifted phenologies during 60 time steps, corresponding to 60 years:

$$MFD_{i(t)} = MFD_{i(t-1)} + \Delta MFD_i$$

Where $MFD_{i(t)}$ is the mean flowering date of species i at time t. ΔMFD_i is a coefficient of phenological shifts sampled for each species in a Gaussian, $\mathbb{N}(0.1, \sigma^2)$ for pollinators and $\mathbb{N}(0.1+\psi, \sigma^2)$ for plants. This coefficient of phenological shifts is in day/year and can be positive, corresponding to a delay of the phenology, or negative, which corresponds to an advance of the phenology in the season. Ψ is a parameter representing the average plant-pollinator mismatch in phenological shifts, while σ^2 represents the heterogeneity in phenological shifts. After the 60 time steps of changes in species phenologies, changes were stopped and the phenologies then remained constant and equal to their new values. Simulations were continued until a second equilibrium was reached (i.e. until the maximum of the variance of species abundances on the last 10 outputs was lower than 10^{-9}, Fig. 1).

We used the *lsoda* solver implemented in the R package *deSolve* (Soetaert *et al.* 2010). We simulated 180 initial random networks of 75 pollinators and 75 plants. Each of these networks was submitted to for levels of ψ, crossed with four values of σ^2 and three levels of intra-guild competition strength (*c*), leading to 8,640 simulations (180×4×4×3). We also performed simulations on networks with 50 pollinators and 50 plants, and with a shorter pollination season, sampling phenologies in $\mathbb{N}$(190,

σ^2_{MFD}=35) instead of $\mathbb{N}(190, \sigma^2_{MFD}=70)$. Thus, at the end we performed 34,560 (8,640×2×2) simulations. In some few cases, less than one plant and one pollinator persisted at the first equilibrium. These simulations were excluded from the following analysis, leading to 33,184 simulations used.

Parameters values used for these simulations are described in Table 1. All the phenological and morphological traits and the parameters of the functional response exhibit inter-specific heterogeneity, except for handling times (β). We did not implement variation on this functional response parameter in order to save computing time, as systems reach the equilibrium much faster when species functional responses differ only on the α parameter.

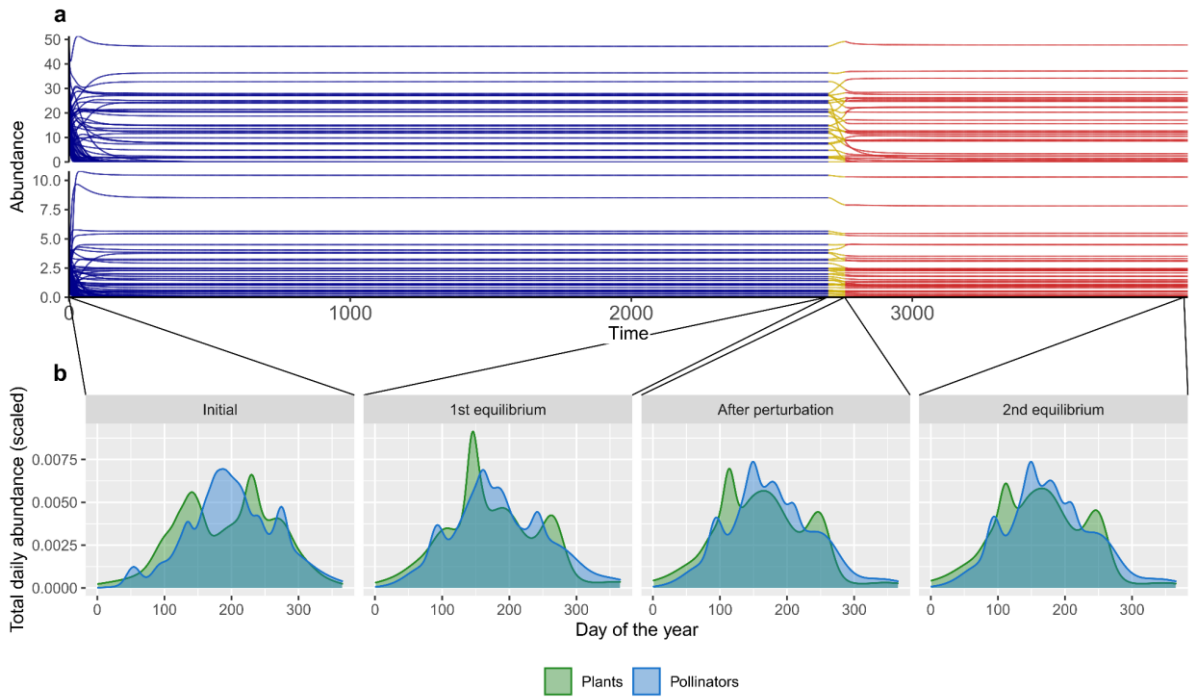

Figure 1: ***Temporal dynamics of species abundances.*** *(a) Temporal dynamics of species abundances, for plants (top) and pollinators (bottom), until the first equilibrium (dark blue), during phenological shifts (yellow) and after phenological shifts until the second equilibrium (red). Here we took $\psi = 0.2$ and $\sigma^2 = 0.2$. (b) Seasonal distribution of plant and pollinator abundances for different times in the temporal dynamics. Abundances are scaled to have an integral equal to one to be plotted together.*

Statistical analysis

Network level analysis

Network robustness is defined as the proportion of persistent species at the second equilibrium compared with the first equilibrium (before phenological shifts). In addition, network resistance is calculated as the proportion of networks without any extinction between the two equilibria for a given set of values of ψ, σ^2, c, n_f, n_p and σ^2_{MFD}.

We investigated how network robustness was related to various network properties: the diversity at the first equilibrium, the nestedness of the interaction matrix at the first equilibrium, and the resilience of the system at the first equilibrium. The nestedness of the interaction matrix at the first equilibrium is the weighted NODF (Galeano *et al.* 2009) of the interaction matrix at equilibrium, after we removed

extinct species and rounded the interaction terms I to the 5th digit to avoid numerical issues. The resilience is the absolute value of the highest real part of eigenvalues of the Jacobian matrix at the first equilibrium. We are interested in explaining how these network variables, as well as season length (σ^2_{MFD}) and intra-guild competition strength (c), affect the network robustness in response to different intensities of average plant-pollinator mismatch and heterogeneity in phenological shifts. Thus, we focus only on the interactive effects between these variables and the levels of average plant-pollinator mismatch or heterogeneity in phenological shifts. To do so, we used a Generalized linear mixed-effect model (GLMM) with a logit link function and a network random effect taking into account that simulations are structured over 180 initial networks:

$$\log\left(\frac{PS_{ik}}{1-PS_{ik}}\right) = \beta_0 + [\beta_1 + \gamma_1 \times diversity_k + \gamma_2 \times season\ length_k + \gamma_3 \times competition_k + \gamma_4 \times nestedness_k + \gamma_5 \times resilience_k] \times mismatch + [\beta_2 + \gamma_6 \times diversity_k + \gamma_7 \times season\ length_k + \gamma_8 \times competition_k + \gamma_9 \times nestedness_k + \gamma_{10} \times resilience_k] \times heterogeneity + \gamma_{11} \times mismatch \times heterogeneity + \varphi_i \quad (4)$$

where PS_{ik} is the proportion of persistent species (i.e. network robustness) in simulation k for network i. β_0 is the intercept, β_1 and β_2 the effects of average plant-pollinator mismatch and heterogeneity in phenological shifts respectively, while γ_{11} is the effect of their interaction. $\gamma_{1\dots10}$ are interaction effects among previously described explanatory variables and average plant-pollinator mismatch ($\gamma_{1\dots5}$) or heterogeneity ($\gamma_{6\dots10}$). All variables were numeric and scaled, to be able to compare their effect size on network robustness.

Species level analysis

To analyze the consequences of phenological shifts for mutualistic interactions and competition within guilds, we first estimated the potential changes in the average strength of mutualism ΔI_k and competition ΔC_k received for each species k. To do so, we compared the interaction strengths of each species k in the interaction matrix I between the first equilibrium ($\overline{I_{eq1_k}}$) and at the second ($\overline{I_{eq2_k}}$), without removing extinct species. The potential changes in the average strength of mutualism for species k is then calculated as $\Delta I_k = \frac{\overline{I_{eq2_k}} - \overline{I_{eq1_k}}}{\overline{I_{eq1_k}}}$. We did similarly to calculate ΔC but using the matrix ω, for pollinators, or θ for plants. Since I and ω matrixes are independent from the abundance of pollinators, and I and θ are independent from plant abundances, it allows to calculate ΔC and ΔI for extinct species too. However, since species abundances are neglected, ΔC and ΔI are only measuring the potential changes in competition pressures and mutualistic interactions, respectively, due to phenological shifts.

We also calculated changes in species abundances ΔN as $\Delta N_k = N_{eq2k} - N_{eq1k}$, where N_{eq1k} (resp. N_{eq2k}) is the abundance of species k in the first (resp. second) equilibrium. Then, to disentangle the effects of competition and mutualism on changes in abundance, we used a linear mixed-effect model explaining changes in abundance (ΔN) by ΔI and ΔC, in interaction with the competition strength of the simulation.

Since data are non-independent as all the parameter combinations were runed on a set of 180 initial networks, we added a random network effect:

$$\Delta N_{jnk} = \beta_{0(c)} + \beta_{1(c)} \times \Delta I_{jnk} + \beta_{2(c)} \times \Delta C_{jnk} + \varphi_n + \varepsilon_{jnk} \quad (5)$$

where ΔN_{jn} is the change in abundance of species *j* in network *n* and simulation *k*. $\beta_{0(c)}$ is the intercept, $\beta_{1(c)}$ is the effect of ΔI and $\beta_{2(c)}$ is the effect of ΔC, all these effects depending on the competition strength *c*. Since pollinator and plant abundances are not on the same scale, we fitted here this model using only pollinators. We also restricted our analysis to cases with either no heterogeneity or no average plant-pollinator mismatch. Thus, we fitted the model detailed in equation (5) for phenological shifts involving only an average plant-pollinator mismatch between plant and pollinators ($\sigma^2 = 0$) and we also fitted the same model for phenological shifts involving only a heterogeneity ($\psi = 0$).

Table 1: *Values of the parameters used in the dynamic model.*

Parameter	Meaning	Value	Variation among		
			species	180 initial networks	Parameter combinations
n_f	Initial number of plant species	50 / 75	-	No	Yes
n_p	Initial number of pollinator species	50 / 75	-	No	Yes
K_i	Flower carrying capacity	~ U(10,600)	Yes	Yes	No
K_j	Pollinator carrying capacity	~ U(1,60)	Yes	Yes	No
m_i	Flower mortality rate	~ U(0.2,0.4)	Yes	Yes	No
m_j	Pollinator mortality rate	~ U(0.8,1)	Yes	Yes	No
α_i	Flower pollen release rate	~ U(0.8,1)	Yes	Yes	No
α_j	Pollinator search rate	~ U(0.8,1)	Yes	Yes	No
β	Saturation term (handling time)	0.9	No	No	No
c	Intra-guild competition strength	0/0.15/0.3	No	No	Yes
MFD_i	Mean Flowering date	~ $\mathbb{N}(190, \sigma^2_{MFD})$/	Yes	Yes	No
MFD_j	Mean Flight date	~ $\mathbb{N}(190, \sigma^2_{MFD})$	Yes	Yes	No
σ^2_{MFD}	Length of the season	35/70	No	No	Yes
SD_i	Flowering period duration (standard deviation)	~ U(5,40)	Yes	Yes	No
SD_j	Flight period duration (standard deviation)	~ U(5,40)	Yes	Yes	No
TM_i	Plant morphological niche centroid	~ U(-1.5,1.5)	Yes	Yes	No
TM_j	Pollinator morphological niche centroid	~ U(-1.5,1.5)	Yes	Yes	No
G_i	Width of plant morphological niche (standard deviation)	~ U(0.1,0.9)	Yes	Yes	No
G_j	Width of pollinator morphological niche (standard deviation)	~ U(0.1,0.9)	Yes	Yes	No
ψ	Average plant-pollinator mismatch	0/0.1/0.2/0.3	-	No	Yes
σ^2	Heterogeneity in phenological shifts	0/0.1/0.2/0.3	-	No	Yes

Results

Our results show that competition strongly mediates the effects of phenological shifts on network robustness, evaluated as the number of persistent species at the second equilibrium, and on network resistance, evaluated as the proportion of networks with strictly positive species abundances at the second equilibrium (i.e. no extinction due to phenological shifts). When there is no competition, very few extinctions occur as a result of phenological shifts, even when the average plant-pollinator mismatch

is high (Fig. 2). When competition increases, network robustness and resistance decrease as a result of both increasing average plant-pollinator mismatch and increasing heterogeneity in phenological shifts. A shorter season length leads to a lower number of extinctions (i.e. higher robustness) in response to phenological shifts. This might be explained by the fact that interaction rewiring, which compensates the loss of a mutualistic partners, is easier in short seasons than in long seasons because of higher synchrony between plants and pollinators.

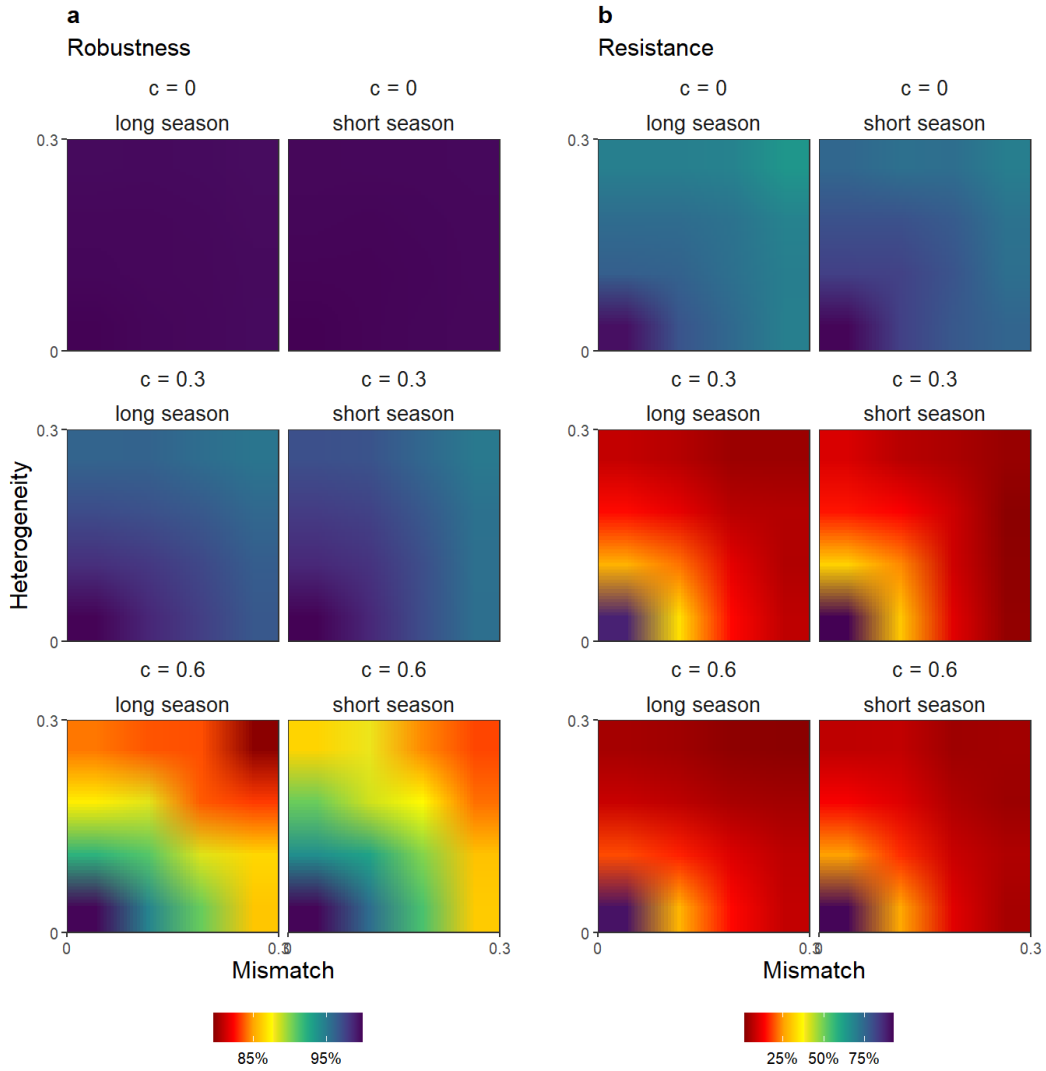

Figure 2: ***Network robustness and resistance in response to phenological shifts.*** *(a) Robustness and (b) resistance are plotted as a function of the heterogeneity in phenological shifts and of the average plant-pollinator mismatch in phenological shifts between plants and pollinators. We plotted one lattice for each combination of competition coefficient and season length, neglecting diversity here. Values are averaged over 360 simulations (180 with initial networks of 75×75 and 180 with 50×50) and linearly interpolated to smooth the patterns.*

By using a logistic regression on network robustness, we show that heterogeneity in phenological shifts, henceforth heterogeneity, and average plant-pollinator mismatch in phenological shifts, henceforth average plant-pollinator mismatch, have comparable effect on network robustness (Fig. 3a).

We also show that they exhibit a positive interaction on network robustness, meaning that combining both dimensions of phenological shifts lead to less extinctions than expected from the additive effects of heterogeneity in phenological shifts and average plant-pollinator mismatch (Fig. 3a). The effects of heterogeneity and mismatch on network robustness are both strongly mediated by competition, higher competition decreasing network robustness to phenology shifts (Fig. 3b). However, while the effects of average plant-pollinator mismatch on robustness do no depend significantly on variables other than competition, the effects of heterogeneity on robustness depend on season length and diversity (Fig. 3c). Diverse communities in short seasons are more robust to increasing heterogeneity in phenology shifts than less diverse communities in long seasons (Fig. 3c). Meanwhile, neither network nestedness nor resilience affects significantly the effects of heterogeneity and average plant-pollinator mismatch on robustness.

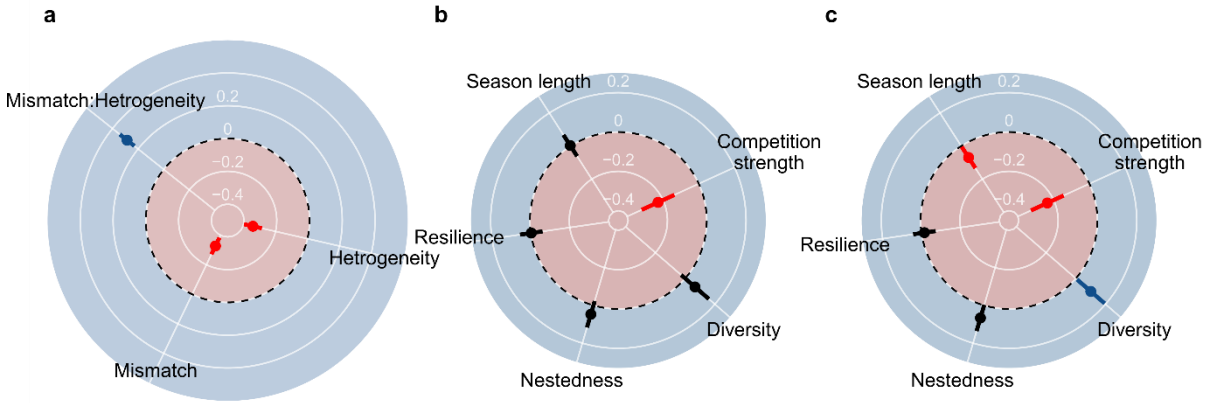

Figure 3: ***Effects of phenological shifts on network robustness as a function of network properties, competition strength and season length.*** *(a) Standardized effects of heterogeneity in phenological shifts, average plant-pollinator mismatch in phenological shifts, and the interaction of both on network robustness (i.e. proportion of persistent species). Effects of interaction between (b) average plant-pollinator mismatch or (c) heterogeneity and network properties on network robustness. Red points correspond to a negative effect on network robustness, black points correspond to non-significant effects and blue points correspond to positive effects on network robustness. Error bars correspond to 95% confidence intervals.*

Both average plant-pollinator mismatch and heterogeneity induce changes in potential competition and mutualism at species level, these changes being highly variable for high values of heterogeneity and average plant-pollinator mismatch (Fig. 4). While the increase of both heterogeneity in phenological shifts and average plant-pollinator mismatch leads on average to a decrease in the strength of potential mutualistic interactions (Fig. 4b & 4d), their effects also partly differ. Heterogeneity leads to more variable changes in competition among species than average plant-pollinator mismatch, while the latter leads to more variable changes in mutualistic interactions than heterogeneity (Fig. 4). Moreover, while average plant-pollinator mismatch does not affect potential competition on average, heterogeneity tends to decrease average potential competition among species (Fig. 4a & 4c).

The changes in potential competition and mutualistic interactions explain well the changes in species abundances (Fig. 5). Changes in potential mutualistic interactions are always the main driver of changes in species abundance. A potential decrease in mutualism logically leads to a decrease in abundance. However, when competition strength is not null and when phenological shifts involve heterogeneity, changes in potential competition become a non-negligible driver of changes in species abundances (Fig. 5a & 5c). In that case, a potential increase in competition leads to a significant decrease of species abundance (Fig. 5b).

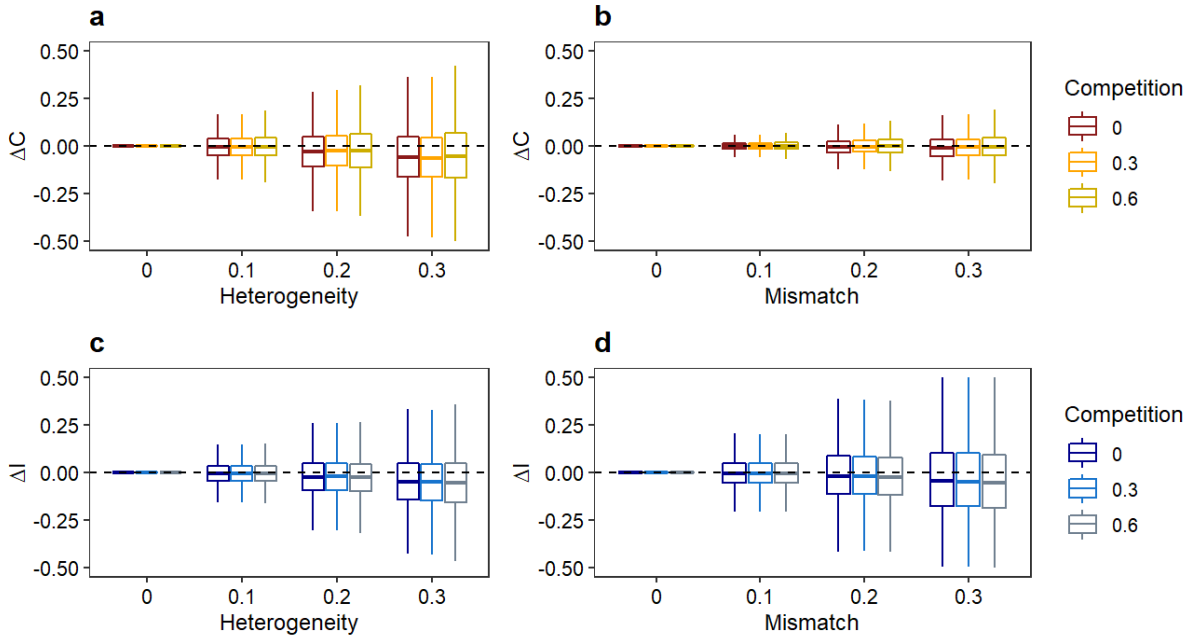

***Figure 4:* Changes in potential competition (ΔC) and in potential mutualistic interactions (ΔI) for different kinds of phenological shifts.** *ΔC as a function of (a) heterogeneity (when $\psi = 0$) or (b) average plant-pollinator mismatch (when $\sigma^2 = 0$), and ΔI as a function of (c) heterogeneity (when $\psi = 0$) or (d) average plant-pollinator mismatch (when $\sigma^2 = 0$). Outlier points were removed to preserve readability.*

Discussion

Our results show that the robustness and resistance of pollination networks to changes in species phenologies are overall equally affected by the heterogeneity in phenological shifts within guilds and by the average plant-pollinator mismatch in phenological shifts. These results show that the heterogeneity in phenological shifts can lead to extinctions even if plant and pollinators are shifting their phenologies with the same average strength. Such results are consistent with previous findings showing that heterogeneity can strongly decrease floral resources available for pollinators (Memmott *et al.* 2007). Empirical studies show that average plant-pollinator mismatch in phenological shifts is non-significant (Bartomeus *et al.* 2011) but that heterogeneity is substantial, shown by high standard deviations in estimated phenological shifts: 0.19 day.year^{-1} over European pollinators (Duchenne *et al.* 2020), 0.26 day.year^{-1} for median flight date of hoverflies in UK (Hassall *et al.* 2017) and 0.28 day.year^{-1} in first

flowering date of British plants (Fitter & Fitter 2002). Surprisingly we find a positive interaction between heterogeneity and average plant-pollinator mismatch on network robustness, suggesting that heterogeneity buffers the consequences of an average plant-pollinator mismatch in phenological shifts. However, as empirical data suggest an absence of average plant-pollinator mismatch, the substantial heterogeneity observed in phenological shifts among species could be an important threat for pollination networks by leading to extinctions.

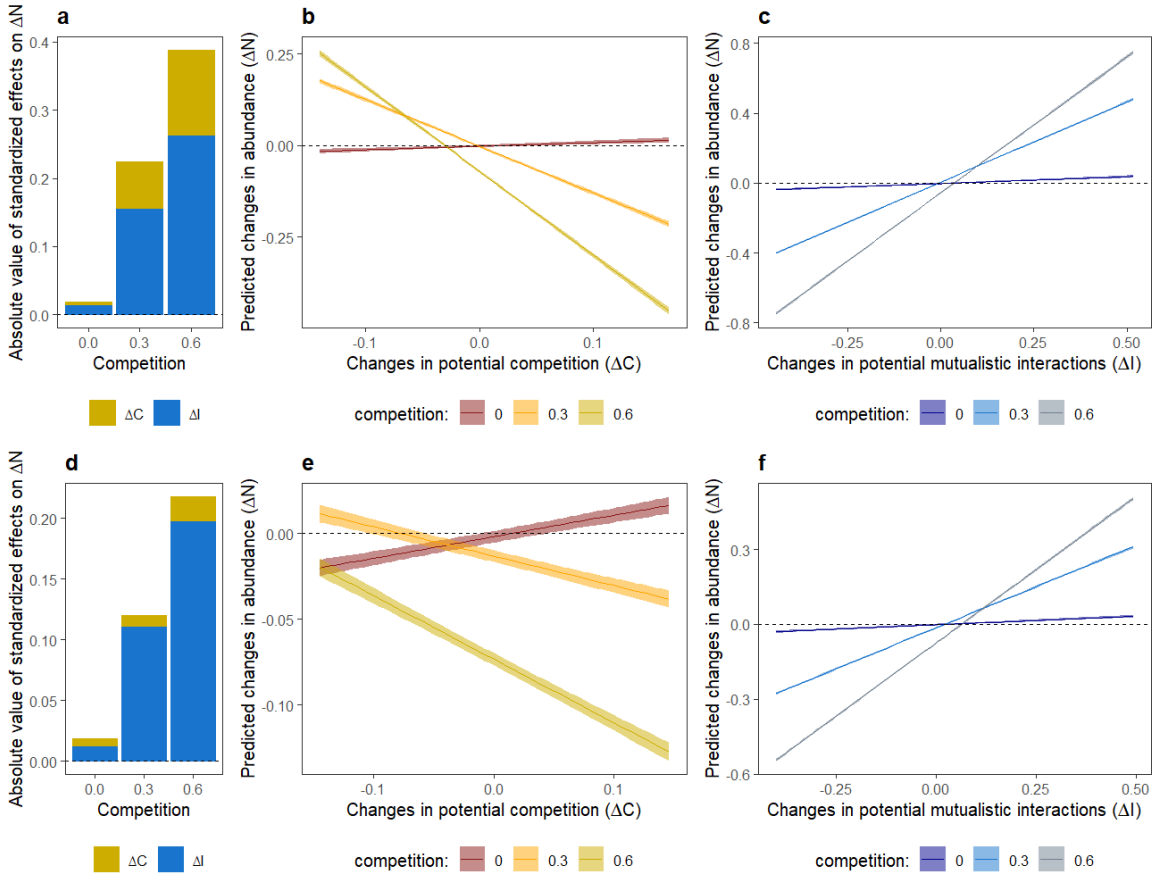

Figure 5: ***Changes in species abundance (ΔN) as a function of changes in potential competition (ΔC) and changes in potential mutualistic interactions (ΔI) for pollinators.*** *The first row (a, b and c) relates to phenological shifts involving only a heterogeneity ($\psi = 0$ & $\sigma^2 > 0$) while the second row relates to phenological shifts involving only an average plant-pollinator mismatch ($\psi > 0$ & $\sigma^2 = 0$). (a) and (d) Absolute values of standardized effects of ΔC and ΔI on ΔN as a function of competition from the linear mixed-effect models defined by equation (5). Predictions from the same models are shown in (b) and (e) for the relationship between ΔN and ΔC and in (c) and (f) for the relationship between ΔN and ΔI. Lines represent the predicted values for ΔN while ribbons represent the 95% confidence interval. Predictions were*

Competition affects both the robustness and the resistance to average plant-pollinator mismatch and to heterogeneity in phenological shifts, increasing competition and decreasing network robustness. Indeed, we find that when competition is null or low, very few species become extinct, while more than 20% of species become extinct when competition is strong. A low competition strength is however sufficient to strongly decrease the resistance of pollination networks, because in that case, at least one or a few species often become extinct when phenological shifts occur. The importance of the competition

in mediating effects of phenological shifts is consistent with previous theoretical results from models on pairs of interacting species (Rudolf 2019). It is also in agreement with empirical results showing that the effect of shifts in flowering phenology on plant fitness is mediated by competition (Alexander & Levine 2019). However, while most previous modeling studies on pollination webs incorporated competition independently from mutualistic interactions (Bastolla *et al.* 2009), we considered here that competition arises within the functional response of the mutualistic interactions as a result of interferences among species sharing the same interacting partners at the same time. This means that competition directly decreases the average strength of mutualistic interactions in our case, explaining also its strong negative effect on species persistence in response to phenological shifts. Indeed, when focusing on the mechanisms that drive changes in species abundances, we find that their main driver is the loss or gain of mutualistic interactions, especially when competition is high. Nevertheless, our results also highlight that changes in competition levels among species can play a substantial role in changes in species abundances when phenological shifts are heterogeneous, while it was widely neglected in previous studies (Memmott *et al.* 2007; Revilla *et al.* 2015).

Our results show that species diversity dampens the negative effects of heterogeneous shifts in phenology among species on network persistence. This positive relationship between diversity and robustness to phenological shifts could be related to wider possibilities of interaction rewiring in diverse communities. Such results echoes empirical ones showing that in a context of heterogeneous phenological shifts, diversity of pollinators prevents temporal mismatch between apple tree flowering periods and pollinator activity periods (Bartomeus *et al.* 2013). The length of the pollination season also affects robustness of pollination networks to heterogeneous phenological shifts, a shorter season increasing the robustness because it increases the phenological overlap between plant and pollinators, and thus allows interaction rewiring too. This result is consistent with previous ones, showing that higher phenological overlap among guilds strongly increases the robustness of pollination network to species extinctions (Vizentin‐Bugoni *et al.* 2020). This result suggests that the decrease in phenological overlaps, observed in plant (Diez *et al.* 2012) and in pollinator (Duchenne *et al.* 2020) communities because of phenological shifts, might affect negatively the robustness of pollination networks to future heterogeneous phenological shifts, because it increases the length of the pollination season. In contrast, neither pollination season length nor diversity affect the network robustness to the average plant-pollinator mismatch, suggesting that diverse communities should be equally sensitive to average plant-pollinator mismatch than less diverse ones.

Here we do not find any effect of network structure, as measured by the nestedness, on network robustness. This results is surprising compared to studies simulating species extinctions directly instead of phenological perturbations, as studies on mutualistic networks found that nestedness increases network robustness to species extinctions (Memmott *et al.* 2004; Piazzon *et al.* 2011). This could be due to the fact that network structure, which corresponds in our model to the structure of the interaction

matrix I, does not encompass all the dimensions of the seasonal structure of the network. Indeed, two pollinators can interact with the same partners, but at different time in the season, thus avoiding competition. Such distinction is likely critical to understand the consequences of changes in the seasonal structure of ecological communities, but it is missed by our measure of network structure as we aggregate interactions over the entire season. This result suggest that the network structure can have distinct effects depending on the kind of perturbation studied highlight the importance to study diverse perturbations and not only to species extinctions (Olivier *et al.* 2020). Moreover, our results also stress the need to develop measures of network structure that encompass the seasonal dynamic of interactions, an overlooked but important aspect of ecological networks.

Moreover, we do not find any correlation between the resilience of networks and their robustness to phenological shifts. This result highlights that this theoretical measure of stability around equilibrium does not predict well the stability of a system facing "realistic" perturbations as here with the simulation of phenological shifts and their consequences on pollination networks. This result echoes a previous one showing that resilience and long-term press perturbations are not closely linked in food webs (Domínguez-García *et al.* 2019). It also supports previous reviews suggesting that stability metrics requiring strong equilibrium assumptions poorly predict stability of system facing "realistic" perturbations (Donohue *et al.* 2016; Kéfi *et al.* 2019).

One has to be aware that the percentage of species becoming extinct because of phenological shifts in our model highly depends on parameter values in the simulations and are thus non informative of what would happen in the reality. However, our model allows to highlight relative results, such as the comparison of the effects of heterogeneity and average plant-pollinator mismatch, and to better understand the mechanisms affecting network robustness or changes in species abundances. We show that even when allowing interaction rewiring, phenological shifts can lead to species extinctions because of joint changes in the strength of mutualistic interaction and competition within guilds. Our results highlight the importance to preserve diverse ecosystems, which should be able to better resist to future perturbations. The current parallel decline of pollinators and plants (Biesmeijer *et al.* 2006; Scheper *et al.* 2014) is thus expected to decrease the robustness of pollination network to the ongoing phenological shifts of plant and pollinators (Roy & Sparks 2000; Fitter & Fitter 2002; Bartomeus *et al.* 2011; Duchenne *et al.* 2020), that could lead to synergistic negative effects on pollination functions and services.

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Global change effects on the temporal dynamics of biodiversity, from species to communities. *The example of plants and pollinators in Europe.*

Abstract:

In our changing world, understanding the cost of environmental changes for species and communities is one of the major challenges of ecology. However, as time series of historical data on biodiversity are rare and often biased in many ways when they exist, turning back the clock to know how species assemblages and their related functions have been affected by global change over the last decades remain a challenge. Here we focused on how species assemblages have been affected by global change, using pollination as a study model and merging analysis of empirical datasets and theoretical approaches. First, we characterized the responses of numerous species to global changes over time: shifts in geographic range and phenology as well as shifts in occupancy, a proxy of species abundance and persistence. By studying temporal dynamics of species response and global change drivers instead of using space-for-time substitution, we were able to assess relative contributions of several global change drivers in those species responses. We highlighted that agricultural intensification and urbanization were the most important drivers of changes in bee and plant occupancies. Our results also suggest that climate warming is a new threat for biodiversity, which is now on par with agricultural intensification and urbanization. In addition, we found that insufficient geographic range shifts led to a decoupling between species historical climatic conditions and their geographic range, which is costly for northern European plants, providing original evidences of the climatic debt assumption. We also showed that changes in occupancy and phenological shifts jointly affect the seasonal structure of pollinator communities, leading to an earlier and shorter pollination season, with lower abundance of pollinators, compared to historical communities. We then investigated how modification of this seasonal structure could affect plant-pollinator interaction networks by using dynamic models. This theoretical approach allowed us to highlight the positive impact of the seasonal structure on diversity maintenance in pollination networks, by balancing competition and facilitation. We also highlighted mechanisms that promote network stability to phenological shifts. Our work provides a set of approaches to try to untangle the complex relations between global change drivers and changes in biodiversity, from species to communities.

Keywords: global change | community ecology | macroecology | phenology | climatic debt

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Effets des changements globaux sur la dynamique temporelle de la biodiversité, des espèces aux communautés. *Exemple des plantes et des polinisateurs en Europe.*

Mots clés : changements globaux | écologie des communautés | macro-écologie | phénologie | dette climatique

Représentation d'un réseau de pollinisation. Gouache sur carton.
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