

## CHAPTER 15

# Predator–prey interactions and climate change

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## 15.1 Introduction: Climate change and trophic networks

Impacts of climate change are observed broadly across genes, species, and ecosystems (Bellard et al. 2012; Scheffers et al. 2016; MacLean and Beissinger 2017). Global temperatures have already increased by up to c1.2°C since preindustrial times. Most predictions qualitatively agree that global warming will cause species extinctions and increase disease transmission (Harvell et al. 2002; Chapters 15, 18). Birds have advanced their breeding or migration phenology (Visser et al. 2004; Kristensen et al. 2015; Møller et al. 2006; Chapter 11), while northward density-shifts in birds have been observed in Fennoscandia (Lehikoinen and Virkkala 2016). Climate change is likely to impact all trophic levels (Chambers et al. 2005), although the response of communities and ecosystems to climate change has only recently received its deserved attention (Lurgi et al. 2012; Pearce-Higgins et al. 2015; Møller et al. 2018; Beaugrand and Kirby 2018). Multispecies interaction networks including predation, parasitism, and pollination (Seibold et al. 2018) cannot be assumed to be linear interactions. Species interact with many others, while these interactions may differ in sign, being either positive (i.e., facilitation) or negative (inhibition). Interaction strength is also functionally important with regard to ecosystem processes, because it encompasses transfer of energy through

an ecosystem, a particularly important feature for community stability (Paine 1980). Climate change is further expected to affect the magnitude of species interactions themselves (Tylianakis et al. 2008; Cahill et al. 2013; Rosenblatt and Schmitz 2016). Biotic interactions are known to play a major role in the maintenance of ecosystems (Bascompte et al., 2006). Climate change will affect species more through shifts in ecosystem functioning (e.g., pollination, mutualism, parasitism) than by its direct effect (Rand and Tscharrntke, 2007; Tylianakis et al. 2008). Furthermore, complex networks of biotic interactions include compensatory mechanisms (Brown et al. 2001) that may buffer the effects of climate change on species (Suttle et al. 2007), but their complexity may also amplify the effects of climate change.

Analysing a single variable (often temperature) for a single life stage of a few selected species may not be satisfactory, therefore, for understanding and predicting the consequences of climate change on the abundance and distribution of organisms (Gilman et al. 2010; Iknayan and Beissinger 2018). A first caveat was revealed by the simple fact that documented advances in breeding phenology of predators may not be in phase with those of their prey (Visser et al. 2004). Examples of differences in phase among trophic levels come from birds feeding on insects (Visser et al. 1998; Pearce-Higgins et al. 2005; see also Devictor et al. 2012), from zooplankton and phytoplankton abundances that have changed at

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different rates (Winder and Schindler 2004), and from animals and plants that have responded heterogeneously to climate change (Nielsen and Møller 2006; Both et al. 2009; Renner and Zohner 2018). A second caveat consists in viewing community response to climate change as the sum of the responses of each individual species (Böhning-Gaese and Lemoine 2004; but see Post and Forchhammer 2002, Devictor et al. 2008), thus considering communities as a ‘super organism’ with its own climate envelopes (Hole et al. 2009; Wilmers et al. 2007; Chapter 16). Indeed, changes in geographic ranges in response to climate change are known to vary in magnitude between taxa belonging to different trophic levels, or to different taxonomic ranks (Huntley et al. 2004), as species ranges result not only from the direct physiological effects of climate (Porter et al. 2000), but also from indirect effects (Pincebourde et al. 2008). It is reasonable to assume that climate change will affect the temporal and spatial association between interacting species at different trophic levels (Böhning-Gaese and Lemoine 2004), because species often show their own response to temperature (climatic niche envelopes). Lastly, range shifts may have cascading effects on community structure and the functioning of ecosystems (Lovejoy and Hannah 2005; Terraube and Bretagnolle 2018). It is thus extremely likely that the impacts of species range shifts will go far beyond those arising from just adding species to or subtracting species from ecosystems. Such changes may produce trophic cascades or lead to ecological catastrophes such as ecosystem phase shifts (Ainley et al. 2015; Ripple et al. 2014). How such changes will resonate at the ecosystem level is particularly difficult to predict and surely represents a challenge for ecologists. Therefore, it is becoming clear that the response at the community level can be expected to differ from species level responses, and the response of one species can hardly be used to predict the response of another, in particular if the latter belongs to another trophic level.

If we are to understand and predict community or species assemblage responses to environmental variability, we must explicitly use a mechanistic approach including species interactions (Voigt et al. 2007). Understanding how climate change will influence the structure of communities and ecosystems

has thus become a major preoccupation for both scientists and managers (Garcia et al. 2014). At the population level, climate change may have important consequences for population regulation, which raises the old question of the respective roles of biotic versus abiotic factors in shaping the regulation of populations and the structure of ecosystems (Martin 2001). The observed effects of climate change on distributions of species has led to the suggestion that biotic factors may be less important than abiotic factors (e.g., temperature), although perhaps more in plants than in animals (Austin 2002).

In this chapter, we first summarize why and how climate change could affect predator–prey interactions. Second, we review the literature about the impact of climate change on predator–prey relationships in birds. A final section will provide prospects for future studies.

## 15.2 Why and how climate change may affect predator–prey interactions

### 15.2.1 Predator–prey relationships and other species interactions

The effects of climate change on host–parasite interactions (Møller 2009; Chapter 15) or plant–herbivore interactions appear to be heterogeneous (McCluney et al. 2012, review in Tylianakis et al. 2008). Climate change often disrupts the synchrony of host–parasitoid phenologies and distributions, phenologically isolating emerging parasitoids from host eggs, which, in the absence of alternative hosts, could lead to localized extinctions, potentially releasing host species from parasitism (Wetherington et al. 2017). Among species interactions, predator–prey interactions are of paramount importance both at population and community levels, because predation is a major cause of mortality in animals, and it is thus a key process in animal population dynamics (Murdoch et al. 2003) and the evolution of life history traits (Doligez and Clobert 2003). Climate change may affect predator–prey interactions through changes in prey or predator abundances, the process of predation itself (including defence against predators), and at the community level through trophic cascades and regime shifts. Parasites,

interacting with climate change, may also have significant impacts on predator–prey interactions. For example, increased temperatures and parasite infection triggered higher prey consumption rates in invasive amphipods, highlighting the potential synergy between parasite infection and temperature and the increased ecological impact inflicted on native communities (Lavery et al. 2017). Much like plant–herbivore relationships, predator–prey interactions can be altered by phenological changes (Visser et al. 2004; Thackeray et al. 2010). It is further common that these two latter interactions actually interact themselves, and often the responses to rising temperature for plants, herbivores, and predators have effects on phenology (either positive or negative), resulting in strong effects on both herbivore and predator population sizes (Durant et al. 2007). However, predators at higher trophic levels are usually disproportionately affected by environmental perturbation compared to plant–herbivore interactions, be it climate change, competition from invasive species, or habitat modification in general (Voigt et al. 2007). Climate change could affect all species interactions in a community, however; given the key functional role of predators, the effects of climate change on community structure and functioning may be driven by the effects of climate change on predators.

### 15.2.2 Processes and mechanisms by which global warming may affect predator–prey interactions

Climate parameters have been shown to affect predator–prey relationships: examples include the Moran effect (synchronizing the pattern of population fluctuations in space; Ranta et al. 1999), or large scale climatic fluctuations such as ENSO or NAO (Stenseth et al. 2002). For example, the interactions between snowshoe hare (*Lepus americanus*) and lynx (*Lynx canadensis*) vary geographically, with regions spatially defined by the influence of NAO (Stenseth et al. 1999). Therefore, it is not surprising that as climate changes, predator–prey interactions are also affected (Bastille-Rousseau et al. 2018). Climate may affect species directly either through a change in life history parameters (such as adult survival or fecundity) or a shift in geographic range or

phenology, or indirectly through the food (prey) of the predator (affecting its abundance: Both et al. 2006), or through the control exerted by the predator on prey (Stevens et al. 2002; Peach et al. 2004). Disentangling the relative contributions of trophic (indirect) and direct climate effects is critical if we are to understand, and more importantly to predict, climate-driven effects at the community (or species interaction) level.

Typically, predator–prey dynamics are described by quantifying changes in the abundance of prey populations as a consequence of direct consumption by predators (the functional response), and the resulting changes in predator abundance as a consequence of energy transfer from prey to predator breeding (the numerical response; Abrams and Ginzburg 2000). The modulating effect of climate on this dynamic has recently received considerable attention. In particular, climate affects consumption rates (Stenseth et al. 2005; Vucic-Pestic et al. 2011), and thus the dynamics of predator–prey interactions (Post and Stenseth 1999; Stenseth et al. 1999). Climatic effects may be as important as top-down or bottom-up effects in shaping predator–prey dynamics (Vucetich and Peterson 2004). In addition, more subtle changes may be expected, as predators also have non-lethal effects on their prey (Lima 1998; Peckarsky et al. 2008) that may also be affected by climate change.

Expected changes on prey or predators may include the following:

- (1) **Changes in distribution.** Changes in distribution may have complex consequences on encounter rate, because both prey and predator, or only one of these, may show a shift in distribution range. The spatial shift may, or may not, be associated with a temporal shift (latitudinal or altitudinal gradient).
- (2) **Changes in phenology.** Depending on whether, and to which extent, temperature is a direct cue of processes affecting the population dynamics of the prey and/or the predator, climate change may result in either a temporal mismatch, or a closer match between predator and prey. Possibly as a consequence of differential changes in species' geographic distribution, or through a change in environmental conditions, several processes could alter the timing of predation

events (e.g., prey and predator encounters), which could have strong direct ecological implications, or indirect behavioural consequences (through non-lethal effects). Because temporal and spatial shifts, though being caused by different climate proxies, will result in patterns of predator–prey interaction that are similar, they will be dealt with simultaneously.

- (3) **Changes in population density.** Population sizes and densities of either predator or prey may change as a consequence of the direct effects of environmental gradual change (temperature rising, changes in precipitation patterns) or extreme environments (catastrophic events).. These changes will occur through climate impacts on vital rates (i.e. survival, breeding success, and dispersal rates). In response, population sizes may change as predicted by classical deterministic models (Murdoch et al. 2003). The direction and magnitude of these changes may differ depending on the shapes of functional and numerical responses (Abrams and Ginzburg 2000), thus varying with the degree of specialization by the predator and the efficiency of energy transfer. Therefore, this will affect the ratio between numbers of predators and prey. Yet, this ratio is of considerable interest here, as a ratio-dependent functional response has been suggested to be more sensitive to the interaction than the Holling functional response (Abrams and Ginzburg, 2000).
- (4) **Changes in behaviour, morphology, or physiology.** These are more subtle changes that are nevertheless expected to be induced by climate change, either through direct effects of climate on predator foraging behaviour or predator avoidance behaviour in prey species, phenotypic plasticity, or microevolution. For instance, diurnal activity patterns of predation behaviour may be affected by climate change, with predators or prey having to cool themselves in particular habitats, or through energetic consequences for individuals. As environmental conditions change, populations may respond by progressively changing their morphological characters (e.g., body size), either due to energetic constraints or physiology. Below we detail these mechanisms.

### 15.2.3 Spatio-temporal effects of climate change on predator–prey interactions

Climate change has the potential to affect the spatial and temporal coincidence of organisms, both potentially leading to disrupted synchrony between predators and prey. Overall, there has been a rapidly growing body of literature exploring how disrupted synchrony affects plant–herbivore interactions (e.g., Bale et al. 2002) and predator–prey interactions (e.g., Logan et al. 2006). While changes in prey reproduction could potentially change predator reproduction, studies have indicated that predators (mainly those preying on insects) become increasingly mistimed in terms of their reproduction relative to the timing of reproduction of their prey (Nielsen and Møller 2006; Both et al. 2009; Chapter 11), resulting in predator breeding cycles becoming mismatched with seasonal peaks in prey availability, with potential consequences in terms of fitness. Although the evidence remains scarce, climate change affects, more or less rapidly, plants, insects, and birds, because of their differential reaction to photoperiod and temperature (reviews in Both et al. 2009; Devictor et al. 2012; Chapters 9, 10). Both et al. (2009) found in a three-trophic level study (caterpillar, four species of passerines that prey upon caterpillars, and a raptor that preys upon the four passerines), that caterpillar phenological response to temperature rising through budburst was on average a delay of only 0.25 days, while passerines lagged 0.5 days after the peak in caterpillar abundance. The Eurasian sparrowhawk (*Accipiter nisus*, hereafter, sparrowhawk) had the largest mismatch of all species considered, which doubled over the 20-year study period.

Despite many studies having investigated how climate change has affected and will affect species distribution ranges, very few of them have specifically examined how differential shifts in range may affect predator–prey interactions (but see Peers et al. 2014). It remains unknown whether distribution shifts are more pronounced in predators than in prey, although this is unlikely since many birds (such as passerines in temperate communities) are both predators (of insects) and prey (of piscivorous raptors). However, it has often been suggested that body size may affect the shift in range because

larger-bodied species may be more resistant to adverse climate and thus less prone to move (Brommer 2008), although some studies maintained that larger species may have a poorer ability to respond to environmental changes than smaller species (Stevenson and Bryant 2000). Raptors eating birds, reptiles, and small mammals are, on average, much larger than their prey, so one may expect that raptors are less susceptible than passerines to being affected by climate change. While most studies on birds have focused on small-bodied species (see section 15.3), recent evidence from raptors suggests that large-bodied species are as affected by climate change as smaller ones, with delays in breeding events or movement shifts towards the north similar to those found for passerines (Lehikoinen et al. 2009). Rough-legged buzzards (*Buteo lagopus*) have responded to ongoing climate change by advancing their laying dates as a consequence of earlier snowmelt in subarctic areas of Finland and Norway (Terraube et al. 2015).

Although the number of studies available still remains scarce, a general finding is a mismatch between prey and predator phenologies due to climate change. Most studies have focused on specialist consumers failing to synchronize with their prey during the breeding period, but little is known about how generalist consumers respond to phenological shifts across multiple food resources and if this could alter food webs through a mechanism other than trophic mismatch. Deacy et al. (2017) showed that, in Alaska, warmer than usual spring periods induced phenological synchrony between two important food sources for Kodiak brown bears (*Ursus arctos middendorffi*). The bears switched from capturing salmon in shallow streams to foraging for berries on the surrounding hills, attenuating a trophic linkage with disproportionate ecological significance.

#### 15.2.4 Climate change effects on population dynamics of prey and predator

##### 15.2.4.1 Effects on numbers

Predators have long been identified as being limited or regulated by their food supply (e.g., Sinclair and Krebs 2002). Climate change is likely to impact

directly upon the abundance of key invertebrate prey for bird predators (Bale et al. 2002). Food availability is a classical limiting factor for the productivity of insectivorous birds (Marshall et al. 2002), and thus its shortage due to global warming may have significant impacts on bird populations, although this has seldom been studied (Pearce-Higgins et al. 2010). For example, Millon et al. (2014) found that a change in trophic interactions overrode the direct climate change effect on cycles of voles eaten by tawny owls (*Strix aluco*, Cornulier et al. 2013). However, recent research in Britain indicated that the negative effects of climate-driven asynchrony on annual productivity did not drive long-term population trends in 21 species of insectivorous birds, which suggested that the relationship between asynchrony and population trends is driven by a wider sensitivity of those species to other environmental pressures (Franks et al. 2018). There are still too few long-term studies that examine the effects of climate change on population growth rates (and not on a single vital rate) of a predator species and its main prey. Nonetheless, these types of studies are indispensable for fully understanding how demographic compensation could affect variation in population growth rates and, ultimately, shifts in species ranges in response to climate change (Villemas et al. 2015).

Both the mean and among-year variance in climate variables such as temperature and precipitation are predicted to change. However, the potential impact of changing climatic variability on the fate of populations has remained largely unexamined. In an analysis of 36 plant and animal species spanning a broad range of life histories and environments, Morris et al. (2008) examined how sensitive long-term stochastic population growth rates were likely to be affected by changes in means and standard deviations of vital rates in response to changing climate. They found that short-lived species (insects and annual plants and algae) were more negatively affected by increasing variability in vital rate relative to longer-lived species (perennial plants, birds, ungulates), and there was no additional effect of taxonomic group. However, in a global assessment of the impact of rapid climate warming and anthropogenic land use conversion on 987 populations of 481 species of terrestrial birds and mammals since 1950,

Spooner et al. (2018) found that declines in population abundance for both birds and mammals are greater in areas where mean temperature has increased more rapidly, and that this effect is more pronounced for birds. Therefore, recent studies strongly suggest that vertebrate predators are being strongly impacted by climate change in combination with other anthropogenic stressors.

#### 15.2.4.2 The complex interplay between density dependence and climate change

It is becoming increasingly evident that population growth of predators is not purely determined by the rate of prey consumption, as usually considered in classic models of predator–prey interactions (Lotka–Volterra or logistic models), but that other factors including social interaction, interference, and territoriality also come into play. More recently, models incorporating ratio-dependent functional responses have been proposed (Berryman 1992). A key factor in modelling the dynamics of predators and their prey is density-dependent regulation, which may occur both in the prey and the predator. For instance, predation rates decrease when predator densities reach their carrying capacity (e.g. Lande et al. 2003). For prey, inverse density dependence, or the Allee effect, is apparently not rare (Stephens and Sutherland 1999). Climate change may affect predator numbers, prey numbers, density dependence in predator numbers, density dependence in prey numbers, and density dependence in the prey–predator interaction itself, or, of course, any combination thereof. In addition, nonlinearity (Henden et al. 2009) and the interaction between intrinsic density dependence and extrinsic environmental variation remains a major challenge in predator–prey interactions (Turchin 1995).

The interplay between density-dependent processes (both acting at the prey and the predator levels) and external factors, such as climate, is a classical problem in population ecology, which is further complicated by the contrasting effects of different types of predator–prey interactions (i.e., specialist or generalist predators, see section 15.2.5.2) and atypical dynamics (such as cycles). Also, the directional trend of climate change (both in average and variance) adds complexity to the analyses. When these factors and their interactions are not

taken into account, they can produce misleading conclusions for the processes at work. A good example is provided by elk (*Cervus canadensis*) population trends in Yellowstone National Park, where a decline in elk followed the reintroduction of wolves (*Canis lupus*), leading to the idea that wolf predation was the key driver of elk decline. However, a more careful analysis (by modelling) concluded that elk decline was influenced by other factors, especially lower than average annual rainfall, rather than wolf predation, which appeared to primarily be compensatory (Vucetich et al. 2005).

Although models and theoretical predictions have been used repeatedly, empirical data (not to mention experimental evidence) are scarce (Wright et al. 2009). While many authors have analysed predator–prey interactions by incorporating density dependence (Sutherland 2006), predation (Evans 2004), or climate (Kausrud et al. 2008), fewer have analysed them together (but see Vucetich et al. 2005, Millon et al. 2014). Theoretical models of predator–prey interactions have been tested with observational data mainly using organisms with short generation times and rapid dynamics, especially invertebrates from aquatic ecosystems, while terrestrial studies come mainly from cyclic dynamics (e.g. Capuccino and Price 1995; Tyson and Lutscher 2016). Climate change is known to be able to drive population dynamics from stable to cyclic dynamics (Coulson et al. 2001), and is also suspected to be the cause of the recent dampening of cycles of small mammals or moths, as well as their predators (review in Ims et al. 2008; Cornulier et al. 2013). Precise quantification of links between climate and cycles (both prey and predator) often rely on limited empirical data. Analysing population models of consumer–resource systems suggested that direct density dependence is primarily related to intratrophic interactions, whereas delayed density dependence in time series may be related to biological interactions. Therefore, numerical changes in delayed density dependence (i.e. the second order autoregressive coefficient) of a predator–prey interaction due to climate change may reflect changes in the strength of predator–prey interaction (Stenseth et al. 2002).

Using large-scale indices of climatic variability as proxies of climate has allowed much progress in

understanding the role of environmental factors on population dynamics (review in Stenseth et al. 2002). For instance, Gamelon et al. (2017) have shown that it is essential to integrate density-dependent feedback into predictive models when investigating the effects of climate change on population dynamics. The variation in the North Atlantic Oscillation (NAO) was also found to interfere with density dependence and predation (Vucetich and Peterson 2004; Wilmers et al. 2006) on the population dynamics of mammalian herbivores. In addition, the same factors acted on driving synchrony (Post and Forchhammer 2004, 2006). Although density dependence, climate, and predation together determine population dynamics, it is clear that mechanistic models are required to understand more thoroughly how these factors interact (Stenseth et al. 2002). Wilmers et al. (2007) have developed a modelling framework to explore the effects of different predation strategies on the response of age-structured prey populations under climate change. They showed that predation acts in opposition to temporal correlation in climatic conditions to suppress prey population fluctuations. However, in some cases predation pressure and climate change appear to interact synergistically to affect negatively the population dynamics of prey species (Pokallus and Pauli 2015).

### 15.2.5. Climate change and the nature of predator–prey interaction

#### 15.2.5.1 Top-down versus bottom-up control

A general and still debated issue concerns whether predators control prey populations (review in Murdoch et al. 2003). In particular the question whether density-dependent or density-independent (in other words, biotic versus abiotic) factors control prey or predator populations has been revived. Whether predators control, or even dampen, prey population fluctuations have mostly been evaluated with models, and to a lesser extent with experiments. Loss of apex predators has been linked to prey release (Soulé et al. 1988) and can lead to alternative ecosystem states (Estes et al. 2011). More generally, prey populations exist at lower densities when exposed to predators (Mech and Peterson 2002).

A meta-analysis of experimental studies suggested that predation usually results in trophic cascades (Schmitz et al. 2000; see section 16.2.5.4). However, the issue of top-down versus bottom-up control of prey populations is still hotly debated (Ripple et al. 2014), and evidence so far suggests that prey control the system more often than the reverse (Vucetich et al. 2005), particularly when anthropogenic pressure induces decreases in apex predators below the density where they carry out structurally important top-down functions (Pasanen-Mortensen et al. 2017).

Regulating processes (either top-down or bottom-up) may change due to climate change (i.e., predators are not regulating prey currently, but could become a regulating factor due to climate change). A nice example is provided by mammalian predator–prey interactions. Although the abundance of migratory caribou (*Rangifer tarandus*) is not controlled by predation (Vors and Boyce 2009), wolves can negatively affect prey abundance when caribou are feeding on resources that are insufficient to maintain high densities. As climate change induces loss of lichen as a winter-food resource (Cornelissen et al. 2001), migratory caribou may face increased predation pressure in the future. But a more complex scenario appears when elk is added to the caribou–wolf interaction, because one of the prey is preferred by wolf, but supports higher predation pressure than the other, the ‘predation pit’ hypothesis (Vors and Boyce 2009). A similar scenario is suggested by Millon et al. (2009) with regard to blackbird (*Turdus merula*) and song thrush (*T. philomelos*), both prey of sparrowhawk, possibly leading to reduced thrush populations. In the case of a mismatch in phenology between prey and predator, it is further conceivable that prey are more prone to respond to temperature increases than the predator, because this gives the prey a new way to escape from predation, and hence a higher selective pressure on prey for early breeding (Both et al. 2009).

#### 15.2.5.2 Specialist versus generalist predators

While specialist predators are mainly dependent on a specific prey species, generalist predators are theoretically able to switch among alternative prey according to their current abundance or profitability

(Andersson and Erlinge 1977). Generalist predation in particular may either stabilize (Erlinge et al. 1988) or destabilize the community (Bonsall and Hassell 1997), depending on ecological conditions. Generalist predators are theoretically expected to maintain relatively constant vital rates because they can shift to alternative prey (i.e., they respond mainly functionally to variation in the abundance of their preferred prey), and therefore should display more stable populations than specialist predators (Redpath and Thirgood 1999). Thus, they are expected to cope better with global changes than specialist predators, which are generally believed to be more sensitive to environmental change than generalists. However, there are very few studies that have shown that specialist predators are more affected by climate change than generalist predators (but see Rand and Tschamntke 2007).

Most studies of predator–prey interactions have involved specialist predators and one or sometimes a few prey species (Korpimäki and Hakkarainen 1991; Nielsen 1999). In addition, most studies involved cyclic predator–prey dynamics of voles and their raptor predators in Fennoscandia (Korpimäki et al. 2003; Lehikoinen et al. 2009). The question thus arises whether the findings can be generalized to more complex food webs (Millon et al. 2009) in other areas. In particular, how generalist predators will respond to changes in their prey community is not predicted by current theoretical models (but see Baudrot et al. 2016), despite generalist predators probably constituting the majority of avian predators (review in Valkama et al. 2005). However, a generalist predator may be partly sensitive to changes in diversity or composition of prey communities. In addition, if generalist predators shift from one prey to another in the community, this may affect interactions among species, both at the level of competing prey and at the level of other predators of the trophic network (Hoy et al. 2017). Very few empirical studies are however currently available, mainly because it is far more difficult to deal with a generalist predator that preys upon dozens of prey species and has to be monitored over many years in order to analyse functional responses (but see Redpath and Thirgood 1999; Rutz and Bijlsma 2006; Millon et al. 2009).

### 15.2.5.3 Functional versus numerical responses

The functional response of a predator largely determines the effect of a predator on the prey population (Abrams and Ginzburg 2000). In addition, the shapes of both numerical and functional responses of predators have strong effects for prey community stability and composition (Jaksic et al. 1992). Predation plays a major role in shaping the structure and dynamics of ecological communities, and the functional response of a predator is of crucial importance to the dynamics of any predator–prey system by linking the trophic levels. However, quantitative and precise studies of functional response are scarce, in particular in the ornithological literature (review in Valkama et al. 2005). In addition there is a great deal of debate on the way we measure functional response and how to ‘scale up’ from local (individual) measurements to a population-level function (Englund and Leonardsson 2008), and a major difficulty remains to measure functional response in the field at (very) low prey density. Finally, both for mammal and bird predators, very few studies have attempted to document variation in the functional response according to season, social status, or sex. Whether climate modulates the functional response remains poorly understood. A few examples have found contrasting effects of abiotic climatic factors (NAO or ENSO) on the functional response of large carnivore species (Sinclair et al. 2013; Bowler et al. 2014).

### 15.2.5.4 Trophic cascades and regime shifts

If climate change impacts upon several trophic levels simultaneously (which is very likely), then wholesale community changes may become evident, and constitute a ‘regime shift’ (Rodionov 2004). Climate change, while affecting predator–prey interactions, may also affect community structure through a trophic cascade (Ripple et al., 2014). In terrestrial ecosystems, trophic cascades result for instance from the indirect effect of predators on plants mediated by herbivores (Paine 1980; Polis et al. 2000). Trophic cascades partly also result from the nonlinear (and thus, non-trivial) nature of species interactions (McCann 2007). They provide examples of how indirect effects propagate in communities via consumption of prey by predators.



Trophic cascades have, however, been more documented in aquatic ecosystems than in terrestrial ecosystems, the reason being unclear, but perhaps related to simplified interactions within each trophic level in the former. A terrestrial example comes from a long-term study of a three-trophic level system including grey wolf, moose, and their winter food resource, balsam fir (*Abies balsamea*; Wilmers et al. 2006). The balsam fir increases in abundance with winter snow (in relation to NAO), and influences wolf kill rates of moose, with cascading effects on balsam fir growth (Post and Stenseth 1999). A virus outbreak in the wolf population allowed testing the transient effects of reduction of predation pressure and climatic variation on the dynamics of this three-level food chain. When wolf numbers dampened, there was a switch from top-down to bottom-up regulation of the moose population, with a stronger influence of climate on moose population growth rate, underlining synergistic interactions between predators (mediated by pathogens) and climate in trophic control. Similarly, a controlled experiment tested how cascading trophic interactions initiated by arthropod predators were affected by changes in rainfall (mimicking climate change) and resulted in leaf litter decomposition changes (Lensing and Wise 2006). More recently, a detailed trophic cascade was analysed in relation to the presence of dingoes (*Canis lupus dingo*; Letnic et al. 2012; Gordon et al. 2016; Morris and Letnic 2017).

### 15.2.6 Adaptation and selection

While most birds apparently have responded to climate change through phenotypic plasticity (e.g., Charmantier et al. 2008), evolutionary responses have also been documented (Parmesan and Yohe 2003; Root et al. 2003; Møller et al. 2004). For example, changes in body size of birds during a period of only 50 years have been detected (Yom-Tov 2001), as well as changes in the proportion of colour morphs in avian predators (Karell et al. 2011). Such morphological changes probably reflect the impact of abiotic conditions and subsequent selection on body size, and this may result in parallel effects of Bergmann's rule on latitudinal trends in body size (Yom-Tov 2001). However, predators are often long-lived, or at

least longer lived than their prey, and, therefore, their biological responses to environmental change may be lagged by one or more generations with respect to their prey (Sæther et al. 2005). Predators are also on average larger than their prey, particularly in aquatic ecosystems as well as in birds (but this is not necessarily true for mammalian predators). Stevenson and Bryant (2000) have suggested with a simple energetic model that small-bodied species will be able to advance breeding dates more easily than large-bodied ones as a response to increasing temperature. These two factors may suggest that larger predators (or longer-lived, which to a large extent is correlated) may take more time to respond evolutionarily to their changing environment than their prey, and therefore may be more vulnerable to climate change in the long term. These differential responses across trophic levels may impact ecosystem functioning, because predators at higher trophic levels may decline more strongly because of the asynchrony with the phenology of their prey (Both et al. 2009).

Finally, it should be borne in mind that predators can also have direct non-consumptive effects on prey and subordinate intraguild predator populations by causing changes in traits such as behaviour and, particularly, habitat selection patterns, growth, and development (Schmitz et al. 2004; Terraube and Bretagnolle 2018). Non-consumptive effects may be equally or more important than consumption for predator–prey population and community dynamics (review in Peckarsky et al. 2008), having indirect effects on other organisms in the community and on ecosystem function (Suraci et al. 2016). The recognized contribution of non-consumptive effects of predators on prey population dynamics may also be affected by climate change, as recently pointed out (Veselý et al. 2017; Lord et al. 2017).

## 15.3 Climate change and predator–prey relationships in birds: the evidence so far

### 15.3.1 Taxonomic bias

More work on the effects of climate change on predator–prey interactions is available for mammals than for birds. In addition, although there is a large literature on small mammal cycles, sometimes

involving avian predators (raptors, owls, skuas), most often mammalian predators are thought to play the key role and have therefore been more studied than their avian counterparts. This is unfortunate because there are fundamental differences between bird and mammalian predators. (1) Raptors are central place foragers, while mammals are not necessarily or only rarely so. Central place foraging leads to differences in the predator–prey relationship, in particular the spatial aspects of predator–prey encounters (Orians and Pearson 1979), energetic constraints (Orians and Pearson 1979), or travel costs. (2) Raptors, like most birds, are socially monogamous, while mammals are mainly polygynous (Caizergues and Lambrechts 1999). As the breeding system may affect population dynamics, and more generally, other life history traits (Bennett and Owens 2002), it is likely that climate change will affect predator–prey interactions in different ways for mammalian and avian predators. In addition, despite the growing evidence that climate change will affect species interactions, most studies in birds have dealt with small-sized passerines (Møller 2002; Peach et al. 2004; Tylisanakis et al. 2008), usually cavity nesters. Fewer studies have addressed bird predators, though numbers are increasing (Rutz and Bijlsma 2006; Millon et al. 2008; Anctil et al. 2014; Terraube et al. 2015; Robinson et al. 2017; Terraube et al. 2017). In this section, we choose to separate studies on terrestrial and marine ecosystems because of differences in the availability of data. Indeed, in marine ecosystems data on prey are difficult to collect and are thus scarce, in contrast to terrestrial ecosystems where climate effects are well documented (Beaugrand and Kirby 2018).

### 15.3.2 Trophic interactions in marine ecosystems

Several studies have focused on the impact of climate change on seabirds (see many references in Jenouvrier 2013), which are often top predators in marine pelagic ecosystems. Because of this trophic position, they have repeatedly been used as indicators of the state of marine ecosystems (Wanless et al. 2007; Ainley et al. 2015). Most seabird studies on the effects of climate change have concentrated on Antarctic and arctic seabirds (e.g. Møller et al. 2006),

with very few concerning tropical (Precheur et al. 2016; Nicoll et al. 2017) or subtropical/temperate seabirds (Sydemann et al. 2015). During recent decades, because of climate change, there have been more El Niño than La Niña events, leading to a generally lower than average Southern Oscillation Index (Murphy et al. 2007; Chapter 2) and, consequently, the Antarctic peninsula is experiencing one of the most rapid warming in the world (Ducklow et al. 2007; Cresswell et al. 2008). The more positive Southern Oscillation Index (Trathan et al. 2007) acts through an increase in sea surface temperature and sea ice season duration and a decreased sea ice extent (Jenouvrier et al. 2003; Ducklow et al. 2007). This may have strong consequences for the entire food web in the southern oceans (Trathan et al. 2007), because these phenomena affect primary production and cause a decline in the abundance and a change in distribution of krill (Euphausiacea).

#### 15.3.2.1 Spatio-temporal effects of changes in prey abundance and distribution on top marine predators

Using a long-term dataset (55 years) of dates of first arrival and laying for the entire community of Antarctic seabirds in East Antarctica, Barbraud et al. (2008) showed that, in contrast to the Northern hemisphere, arrival and laying dates of Antarctic birds are delayed as a consequence of reduced krill abundance and delayed access to colonies resulting from late sea ice breakup. King penguins (*Aptenodytes patagonicus*) forage over the polar front and dive to the thermocline to feed on myctophid fish (Péron et al. 2012). Here, climate change affects the position of both the polar front and the thermocline, showing that climate change in polar marine ecosystems not only impacts horizontal, but also vertical, prey distribution through modifications of sea temperature and sea ice extent. In both studies, the distance to foraging areas is affected and, if increased, may have a negative impact on breeding success (Durant et al. 2007) because of longer foraging trips during the breeding season and thus reduced parent and chick body conditions (Trathan et al. 2007). Climate change has already increased water temperature in the Norwegian Sea and thus modified currents and shifted the herring stock to the north, far away from breeding grounds of puffin

(*Fratercula arctica*), thus creating spatial mismatch between prey and predator (Durant et al. 2007). Although a warming climate may change the distribution of prey for little auks (*Alle alle*), they may not be negatively affected, because their energy expenditure will decrease with increasing temperature (Amélineau et al. 2018). Further research is urgently needed to understand how different anthropogenic stressors like overfishing, pollutants, and climate change interact to affect prey availability and distribution and how they reverberate into seabird demography. This is key to assess seabird resilience to global change and to prioritize conservation efforts (Oro 2014).

#### 15.3.2.2 Effect of climate change on top marine predator life-history traits and predator density and demography

In the Southern Ocean, some marine predator populations show periodicity in population and breeding performance, driven by physical forcing from, e.g., the El Niño–Southern Oscillation, ENSO (Jenouvrier et al. 2009; Ducklow et al. 2007). During the late 1970s, change in population periodicity and sudden variation in population trends have been recorded, indicating a regime shift in the Southern Ocean (Chapter 2), potentially driven by climate change. Furthermore, during warm anomalies, birds skip breeding probably because the food availability was low and limiting for the highly energy demanding reproductive activities (Jenouvrier et al. 2003). Cresswell et al. (2008) showed that rapid changes in the mean supply and the patchiness of krill could have an effect on female and chick condition and thus on breeding success of macaroni penguins (*Eudyptes chrysolophus*). Few studies have reported a decline in avian prey quality due to climate change in marine ecosystems. Wanless et al. (2007) reported that climate change impacts the breeding success of black-legged kittiwakes (*Rissa tridactyla*) by affecting the quality of prey, i.e. lower condition of the sandlance (*Ammodytes marinus*). Climate change has also been shown to decrease adult survival in the little auk in the Arctic through a change in prey quality or quality (Hovinen et al. 2014). Hilton et al. (2006) studied the effects of climate change on the rockhopper penguin (*Eudyptes chrysocome*), which has experienced a marked

population decline throughout most of its circumpolar breeding distribution. Using stable isotope analyses and feather samples dating back to 1861, they found evidence for a decreased signature in primary productivity over time. This decline was associated with annual variations in sea surface temperature, and may reflect a reduced carrying capacity for penguin populations.

Changes in prey abundance, distribution, and quality due to climate change have affected the life history traits of seabirds, and, overall, there is a spatial mismatch between the distributions of seabirds and their prey leading to longer foraging trips. A recent meta-analysis of 209 phenological time series from 145 breeding populations evidenced that, between 1952 and 2015, seabird populations worldwide have not adjusted their breeding seasons over time or in response to sea surface temperature (Keogan et al. 2018). This limited temperature-mediated plasticity of reproductive timing highlights the high vulnerability of marine top predators to future mismatch with lower-trophic-level resources.

### 15.3.3 Bird predator–prey interactions in terrestrial ecosystems

#### 15.3.3.1 Changes in phenology and their consequences for predators

Many studies of the impact of climate change on terrestrial birds have revealed a mismatch between advancing food abundance peaks and the timing of highest energy requirements for the nestlings (Both et al. 2009; Burgess et al. 2018), although only 37 per cent report a negative effect on reproductive success (Chapter 9). When early spring temperatures are high, European insectivorous passerines tend to lay their first egg earlier to match peak food abundance (Cresswell and McCleery 2003). Climate change also has an effect on the timing of migration (Chapter 8). In North America, southward migration of sandpipers and falcons were expected to be strongly related to timing of snowmelt (Niehaus and Ydenberg 2006). However, sandpipers seem to respond less strongly than their falcon predators to variation in timing of snowmelt, leading sandpipers (adults and juveniles) to encounter more predators on their stopover sites. These different effects of

earlier snowmelt indicate that climate change could alter the ecological dynamics of predator–prey systems (Niehaus and Ydenberg 2006).

### 15.3.3.2 Changes in prey accessibility and availability, and effects on predator foraging success

Birds feeding on soil-dwelling invertebrate prey have to forage in dry surface soil as climate change generates high temperature and low rainfall. Indeed, dry surface soil makes it more difficult for birds to probe, and soil invertebrates tend to bury themselves deeper in the ground and thus become inaccessible to predators (Peach et al. 2004). The induced food shortage has consequences for bird condition and thus for breeding success (Peach et al. 2004; Green 1988). Additionally, so far few studies have investigated the effects of climate on bird foraging success during the non-breeding period. Terraube et al. (2017) showed that, in boreal ecosystems, increased frequency of rainy days in autumn influences the foraging success of pygmy owls (*Glaucidium passerinum*), potentially through reduced vulnerability of small mammals to predation in rainy weather. In this case, climate change is making prey inaccessible, or at least less accessible, to avian predators. In contrast, other authors have reported potential benefits of global warming for avian predators, such as increased prey availability in aquatic ecosystems. Stevens et al. (2002) described a possible improvement of foraging success by snail kites (*Rostrhamus sociabilis*) in an increasing temperature scenario in Florida wetlands. The snail kite is a specialist predator of apple snails (*Pomacea paludosa*). At low water temperature, apple snails become inactive and tend to bury themselves, while at higher temperature apple snails are active and consequently become accessible. Nevertheless, severe drying events render apple snails unavailable for kites (Stevens et al. 2002). If water temperature increases due to global warming, it is easy to imagine a shift in snail kite distribution to the north, advancement in laying, or an increase in breeding success due to an improvement in apple snail availability and in foraging success of snail kites. In crag martins (*Ptyonoprogne rupestris*), high temperatures during brood care lower breeding success, because drought

decreases availability of aquatic insects for offspring (Acquarone et al. 2003).

### 15.3.3.3 Generalists versus specialist bird predators

Generalist predators are expected to cope with climate change better than specialists (see section 15.2.5.2). However, the few studies available so far indicate that generalist avian predators are not necessarily able to shift to other prey species (e.g. sparrowhawks in Nielsen and Møller 2006). Two studies involved raptor generalist predators. In Denmark, a long-term study of sparrowhawks, one of the most common bird-eating predators of the Palearctic, showed they have experienced important changes in the composition of their prey community during the last 40 years (Millon et al. 2009). Contrary to expectations for a generalist predator, sparrowhawks seemed to be predominantly sensitive to changes in the abundance of only two main prey species (skylark, *Alauda arvensis*, and black-bird, *Turdus merula*). In another generalist predator, the common buzzard (*Buteo buteo*), Lehtikoinen et al. (2009) found that climate had a much stronger effect than vole abundance on timing of breeding in the raptor. The buzzard, though breeding at the northernmost limit of its range in Finland, should have benefited from increased temperatures during the breeding season. Interestingly that was not the case, as the Finnish breeding population has crashed, possibly partly due to asymmetrical climate change, i.e. an increase in winter and early spring temperatures on the one hand (leading to earlier breeding), but no such warming in late spring and summer temperatures on the other hand (leading to poor meteorological conditions during chick rearing and ultimately lower productivity). Gilg et al. (2009) reported a study about the impact of climate change on cyclic predator–prey population dynamics in the high Arctic. In this case, the long-tailed skua (*Stercorarius longicaudus*) and the snowy owl (*Bubo scandiacus*) feed almost exclusively on lemmings (*Dicrostonyx groenlandicus*), and so they could be classified as specialist predators. Until 2000, lemmings displayed regular 4-year cyclic dynamics, but afterward, the density of lemmings has remained at a low level (Gilg et al. 2009). As a consequence, the snowy owl has been absent since 2000. Gilg et al.

(2009) ran models with different climate change scenarios and showed that in all cases climate change will lead to an increase in the duration of the lemming population cycle and a decrease in the maximum population densities, which may ultimately lead to local extinction of the owl (Schmidt et al. 2012). Overall, contrary to predictions, studies showed that generalist predators may not cope better with climate change than specialists.

### 15.3.4 Concluding remarks on the impact of climate change on bird predator–prey interactions

Studies of the effects of global warming on predator–prey interactions in marine ecosystems have investigated almost exclusively bottom-up processes. Through an effect on prey, global warming indirectly affects many life history traits and demographic parameters of seabird predators. In terrestrial ecosystems, studies mainly focused on the match–mismatch processes in insectivorous birds of Europe or North America, although recently several studies involved raptors. Both in marine and terrestrial ecosystems climate change has started to affect avian predators and has already had significant effects on several aspects of avian predator–prey interactions. Few studies have detailed the effects of climate change on both prey and their avian predators, with the exception of tits and caterpillars (Both et al. 2009; see also Nielsen and Møller 2006), and few have identified by which mechanisms such effects have occurred. However, Terraube et al. (2015) showed that climate change impacts rough-legged buzzards in Lapland indirectly through a climate-driven decrease in the abundance of their main prey (voles) and not through direct negative effects of adverse weather on nestling survival and breeding success. A similar conclusion arose from a study focusing on tawny owl population dynamics (Millon et al. 2014).

## 15.4 Future prospects

Despite the recognized and acknowledged importance of the effects of climate change on trophic interactions, there are too few studies currently available to suggest any clear general trend (Gilman

et al. 2010). In addition, given that the detected effects are sometimes in opposite directions, and that changes observed in one species may indirectly affect other parts of the community through competition or predation, it is currently almost impossible to predict the future effects of global change at the community level using predator–prey interactions. Below we list areas that we believe should be tackled in the near future.

### 15.4.1 Long-term studies

We need more long-term field studies of communities (Jenouvrier 2013). Although there are several models and theoretical approaches that predict effects of climate change on communities, few empirical data support these models. Therefore, it is essential to emphasize the need for maintenance of long-term biological datasets to validate predictions. In addition, new studies should be started and carried out in poorly studied although important ecosystems, such as the tropics, where climate change is nevertheless acting (e.g., Chamaille-Jammes et al. 2008). Recent research revealed strong interactive effects of climate and land-use change on ecological communities in tropical grasslands and savannahs (Newbold 2018), highlighting the need to better assess the consequences of these modifications in community structure in terms of trophic cascades and ecosystem shifts. The relationship between climate and population cycles suggests a causal relationship between climate change and cycle dampening for small mammals and their predators, as well as insect cycles (Jepsen et al. 2008). Again, long-term studies may reveal unexpected patterns. Since the mid 1990s, small mammal cycles have dampened in Fennoscandia (Ims et al. 2008), but more recent data suggest that cycles may restart again, at least in the boreal zone (Brommer et al. 2010; Cornulier et al. 2013). Long-term empirical studies could help shed light on other poorly understood aspects like how individual variability in predator behaviour may modify the effects of climate change on predator–prey interactions. This would improve our ability to predict the demographic response of both predators and prey species to environmental change (Pettorelli et al. 2015). Finally, we need a better integration between observational,

experimental, and modelling studies on mechanisms of species interactions along environmental gradients.

### 15.4.2 Modelling and experimental studies

Above all, we need more studies that apply a mechanistic approach, because it allows us to gain understanding of underlying causes (Sutherst et al. 2007). To date, there have been few modelling attempts to predict the effects of climate change on predator–prey relationships. Such models may help to address complex issues such as trophic cascades, hyper predation processes, and compensation, so far poorly studied in the context of global warming (but see Emmerson et al. 2005). While the relative importance of deterministic and stochastic factors has been a central tenet in population ecology for at least five decades (see Coulson et al. 2004 for a summary), the theoretical debate in predator–prey ecology moved from deterministic models to individual-based models, stochastic and numerical models (van der Meer and Smallegange 2009; Bocedi et al. 2014). Indeed, even simple individual-based models including predator–prey interactions may help in understanding how climate-driven changes in distribution or breeding phenology of prey may have population consequences for predators (Peers et al. 2014). In addition, modelling studies would help answer questions about how climate change affects the synchronization of breeding phenologies, and how it will affect population dynamics when individual heterogeneity (and variance in fitness) is taken into account. Recent advances in evolutionary models will help disentangle these effects. Similarly, recent methodological advances integrating principles from consumer–resource analyses, resource selection theory, and species distribution modelling, will enhance quantitative prediction of shifts in species range (Pellissier et al. 2013; Trainor and Schmitz 2014).

### 15.4.3 Evolutionary questions and conservation issues

Given that predator–prey interactions are often viewed as an evolutionary arms race, the effects of global warming on predator–prey interactions beg for evaluating its longer-term, evolutionary implications.

For instance, the mismatch in phenology between prey and predator may lead to counterintuitive selective pressures. For example, it remains to be studied whether predators are phenotypically plastic with regard to prey choice, whether prey are able to cope rapidly with a changing predator community, and at which rate microevolutionary change could allow either prey or predator to cope with its changing environment. Thus we need better analyses of the effects of temporal and spatial climatic variation, and quantification of species traits in species interactions. With regard to the interaction itself, apart from being specialist or generalist predators, there is also a gradient in how predators acquire and use food for reproduction (i.e., the income vs capital breeder dichotomy), which has strong effects on life history traits of predators. Very few studies of birds have studied whether this difference in processing and using energy is affected by climate change, although it is likely.

Shifts in predator–prey dynamics can trigger trophic cascades and affect communities at large scale with conservation implications worldwide. For example, in the Arctic polar bears (*Ursus arctos*) have recently been recorded shifting to foraging on nesting seabirds because of sea-ice loss and, consequently, lower access to ringed seals (Iverson et al. 2014). This has potential consequences for large-scale population dynamics of seabirds and the whole Arctic food web. Similarly, the dynamics of small rodent species, such as voles and lemmings, that were previously characterized by large amplitude regular cycles has recently changed more or less simultaneously across Europe (Ims et al. 2008). Thus, climate change could affect predators indirectly through modifications in population dynamics of voles (Solonen 2006). As a consequence, specialist predators of cyclic rodents have already declined (Millon and Bretagnolle 2008). Changes in small herbivore dynamics have the potential to lead to a regime shift, thus representing a new challenge for the conservation of biodiversity. The life histories of predators are seemingly adapted to these interactions (Ims and Fuglei 2005), but it is unknown to what extent their populations can be sustained under different dynamics. Worryingly, models in Gilg et al. (2009) showed that prey–predator communities will be severely impacted by climate change. Further

research is also needed to understand the effects of conservation actions (e.g., protected areas establishment and management) on the resilience of predator–prey interactions under climate change and how this reverberates at the community and ecosystem scales. Most of the available evidence comes from marine reserves (Ling and Johnson 2012), but the effects of protected areas on predator–prey interactions in terrestrial ecosystems and their potential buffer effect against climate change remains virtually unknown. Does the maintenance of complex food webs in protected areas help buffering ecosystems against regime shifts?

As a consequence of their life history traits, predators are supposed to be more affected by the adverse effects of climate change than lower trophic levels. Indeed, many emblematic predators, such as raptors, are already of conservation concern (see, e.g., Bennett and Owens 2002 for a comparative analysis on birds; McClure et al. 2018). These concerns, and the ongoing climate-driven shifts in trophic interactions, may have important consequences for population dynamics, community structure, and ecosystem resilience, posing a challenge for conservation in the near future.

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