Climate change and trophic interactions

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'The balance of evidence suggests a discernible human influence on global climate'[1]. How this will influence the ecosystems of the world is a major preoccupation of many biologists who are charged with providing policy makers with evidence of the need for, and type of, remedial action. Although there is no doubting the complexity and importance of the issue, most studies have concentrated on the effects of a single variable (usually temperature) on one genotype and life-stage of a given species and ignored the plethora of possible ecological interactions within and between the abiotic and biotic components of climate change. The potential for misleading inferences from such studies has been highlighted[2].

Here, we review work that has begun to address one aspect of this problem of natural complexity by considering more than one trophic level. Some theoretical implications of climate change on interacting species have already been investigated, concluding that density dependence and species interactions might play major roles in determining the magnitude of changes in mean density in response to climate change[3,4]. We draw largely on examples from studies of insects and their host plants and concentrate on data indicating effects of climatic warming on shifts in phenology or distribution. Because species show individualistic responses to temperature, carbon dioxide (CO_2) concentration and other environmental variables[5,6], it is reasonable to assume that climate change will affect the temporal and spatial association between species interacting at different trophic levels.

The current accelerated climatic warming is largely caused by emission of so-called 'greenhouse gases', chief among which is CO_2. The studies cited here relate explicitly (through experimental manipulation) to temperature-driven effects on intertrophic associations or implicitly (through empirical analysis of long-term data) take account of changes in a range of factors. As well as its indirect impact through raising temperature, CO_2 can also affect trophic interactions directly. Elevated CO_2 concentrations lead to decreases in leaf nitrogen and increases in carbohydrates and phenolics, and the effect of these changes on interactions between plants and their insect herbivores has recently been reviewed[7]. However, there are very few studies relating these effects specifically to temporal or spatial associations between trophic levels. Such associations could be disrupted if elevated CO_2 concentrations differentially affect development rate of host plants and their insect herbivores. Of the 49 insect–plant interactions reviewed, developmental time of insects at elevated CO_2

With confirmation of anthropogenically induced climate change, the spotlight is on biologists to predict and detect effects on populations. The complexity of interactions within and between the biotic and abiotic components involved makes this a tough challenge, and most studies have consequently considered effects of only single climate variables on single species. However, some have gone further, and recently published long-term datasets now offer opportunities that complement new experimental approaches that span trophic levels. With these datasets, predicting relative shifts in temporal and spatial associations could be among the most tractable problems.

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concentrations was unaffected compared with ambient CO_2 concentrations in 36 cases, increased in ten cases and decreased in three cases[7]. Depending on the plant species, flowering times could be earlier or later under elevated CO_2 compared with ambient concentrations[8]. This might lead to a decoupling of the phenology of plants and their pollinators[8], although in the broad bean (*Vicia faba*) it has been shown that flowering starts earlier and finishes later at elevated CO_2 concentrations compared with ambient[9].

Effects of climatic warming on temporal associations

Factors affecting the relative timing of host–plant and herbivore phenologies have been examined in great detail, particularly the implications for plant damage. This work has mainly concentrated on the timing of budburst and the need for insects to commence feeding after hatching or terminating diapause. If eggs hatch long before budburst, insects will generally fare poorly on deciduous hosts, for obvious reasons. If eggs hatch after budburst, insect success will be partly determined by the interval between budburst and the commencement of feeding, because leaf quality usually declines with leaf maturation. Early or late egg hatching relative to budburst could therefore lead to a reduction in plant damage.

The psyllid *Cacopsylla moscovita* provides a good example of the complexity of interactions[10]. The nymphs feed only on catkins of creeping willow (*Salix repens*) and can take the whole period of catkin development to mature to adulthood. Also, the female must place the egg in a protected situation between the developing catkin ovaries, so it is essential that eggs are laid as soon as catkins appear and that the eggs hatch almost immediately. The psyllid stores mature eggs for at least six weeks before laying, providing a buffer against changes in the phenology of catkin appearance. Experiments on related species show that a rise in temperature will increase the rate of development of psyllids proportionately more than that of catkins[11], favouring survival of the psyllids in a warmer climate.

A direct link between the physiological status of the host plant and initiation of insect feeding would provide the safest method of ensuring appropriate herbivore phenology, regardless of climatic factors, but it rarely seems to happen. There is no evidence of egg hatch being controlled directly by the physiological status of the host plant, although termination of diapause in the feeding stages can sometimes be influenced in this way[12]. An alternative solution for the herbivore would be to use the same cues to

initiate feeding as those used by the host plant to initiate growth. Intuitively, this must happen, but there are few examples where cues have been quantified for different trophic levels. In the case of gall midges (Cecidomyidae), the period of sensitivity to temperature cues differs between trophic levels, leading to large variations in synchronization between years and the need for the herbivores to be tolerant of a range of leaf ages[13].

Budburst in most temperate trees requires a period of chilling followed by warming[14]. Some trees have a large chilling requirement, and for every reduction in the number of chill days experienced there is a large increase in the thermal time required for budburst. Others have a low chilling requirement with relatively little effect of the number of chill days on thermal time to budburst. In the latter case, climatic warming can considerably advance budburst, because the chilling requirement is still likely to be met but the thermal time required will be achieved more quickly. In the former case, however, more thermal time might be needed because optimum chill levels have not been achieved, leading to similar, or even later, budburst in a warmer climate.

Diapause termination or egg hatch in insects might also require a period of chilling followed by an accumulation of heat units[12]. Winter moth (*Operophtera brumata*), which attacks oak (*Quercus* spp.) and other food plants, provides a well studied example. In oak, the date of budburst is strongly correlated with the 'thermal time' above a threshold temperature over the previous ten days; this threshold decreases as daylength increases[15]. Hence, because photoperiod at a given date remains constant, climate warming could advance budburst in oak. Egg hatch in winter moth is related to thermal time from spring[16]. It begins after 292 day-degrees above a threshold of 3.9°C have elapsed from March, leading to the expectation of earlier egg hatch under milder conditions. This might help to maintain synchronization with advancing budburst in oak. However, the possible influence of previous chilling was not considered in either the oak budburst study[15] or the winter-moth egg hatching study[16] and so the synchronization might be disrupted if climatic warming leads to a suboptimal chilling period in oak but not winter moth, or vice versa.

The effect of climatic warming on the relative timing of egg hatch in winter moth and budburst in pedunculate oak (*Q. robur*) has recently been investigated experimentally[17]. At elevated temperature (i.e. ambient +3°C), eggs hatch about eleven days earlier than at ambient temperature. Budburst is similarly advanced, the conclusion being that climatic warming would not lead to dissociation. A different outcome was predicted on Sitka spruce (*Picea sitchensis*), because budburst in this host plant is not expected to change greatly with increasing temperature, leading to early egg hatch of winter moth relative to budburst[18] (Fig. 1). In the study on *Q. robur*[17], no direct effects of elevated CO_2 concentrations on the relative timing of budburst and egg hatch in winter moth were found.

Local genetic variation in egg hatch and budburst phenology could help buffer any differential effect of climatic warming[16,19]. Maintenance of associations will thus be influenced by the speed of adaptation of the moths to gradually changing average temperatures, through redistribution and selection of appropriate genotypes.

Any reduction in larval density resulting from phenological changes is likely to affect higher trophic levels. For example, the chicks of birds such as tits (Paridae) depend heavily on winter-moth larvae for food. Indeed, great tits (*Parus major*) are able to adjust the phase of their breeding
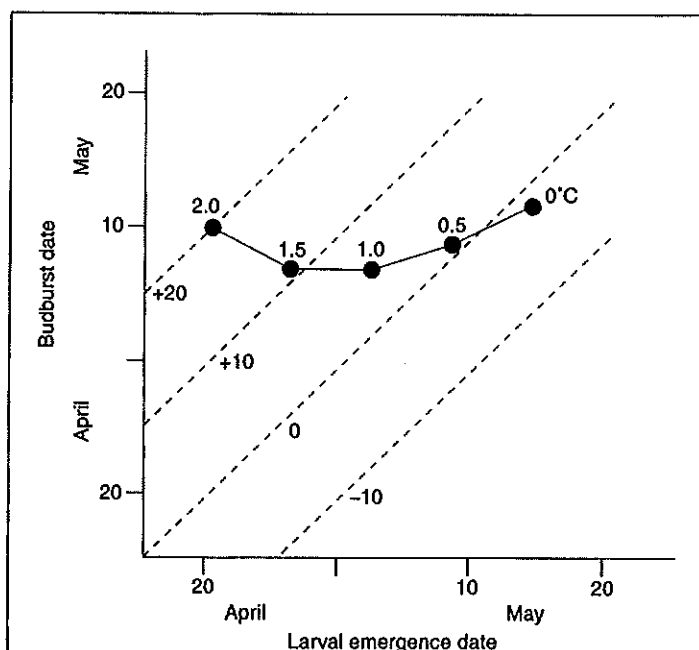

Fig. 1. Mean predicted dates of budburst on young Sitka spruce (*Picea sitchensis*) and larval emergence of winter moth (*Operophtera brumata*) at Braemar, Scotland, averaged over the period 1912–1978, corresponding to uniform warming of 0.0 to 2.0°C. The broken lines are contours of the asynchronization (−10, 0, 10 and 20 days) between larval emergence and budburst. For example, for 2°C warming, mean larval emergence date is on 20 April and mean budburst is on 10 May, giving an asynchronization of 20 days. *Reproduced from Ref. 18, with permission.*
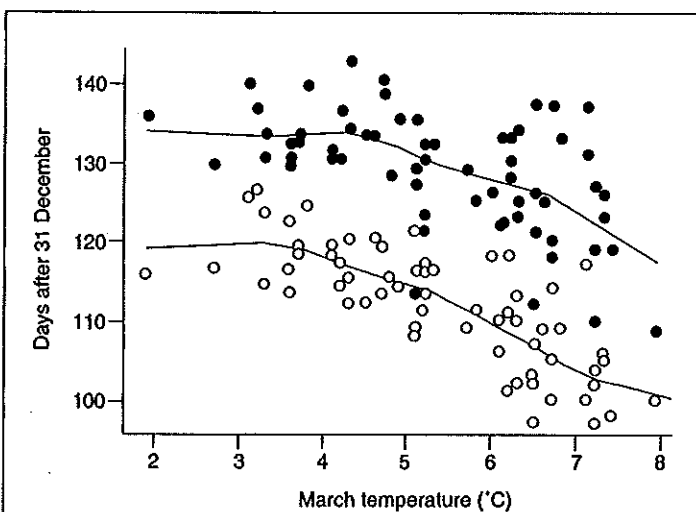

Fig. 2. The effects of March temperature on the mean date of first flowering (number of days after 31 December) of garlic mustard (*Alliaria petiolata*; open circles), and mean first appearance date (number of days after 31 December) of the orange tip butterfly (*Anthocharis cardamines*; filled circles), from 1883 to 1947. Data points are means for England and Wales. The smoothed lines are created by the LOWESS (locally weighted scatterplot smoothing) process. *Modified, with permission, from Ref. 25.*

cycles to some extent to maximize the supply of winter-moth larvae[20]. However, the birds are unable to keep pace with increasing larval development rates at higher spring temperatures[21,22], because selection for earlier egg laying occurs as a result of the effect of higher spring temperatures on larval availability, but cues operating to initiate egg laying by the tits do not predict spring temperature[22].

Box 1. Phenological datasets

There is no definitive list of phenological sources. Many schemes are the property of individuals or organizations concentrating on individual taxa. Schemes that involve more than one trophic level are rare.

A very recent survey by Bussay[29] of European countries, via their meteorological institutes, indicated that regular phenological observations or networks existed in 22 of the 28 countries responding. In the majority of cases, these are organized by the meteorological or hydrometeorological bodies of those countries. Examples of schemes using clonal plant material are the International Phenological Gardens and the Global Phenological Monitoring Network, both international projects coordinated in Germany. The Deutscher Wetterdienst (Germany) includes native plants, whilst schemes including both botanical and zoological interests (such as the Slovak Hydrometeorological Institute) are less common. However, Bussay's survey[29] was targeted and underestimates the extent and type of current recording. For instance, the UK submitted a null return, but we are aware of the following schemes that can provide phenological data. The potential links between schemes have been examined in only a few instances.

Source	Taxa	Scope
British Trust for Ornithology	Birds	National, 50+ years
University of Oxford, Zoology	Birds and caterpillars	Local, 50+ years
Institute of Arable Crops Research	Aphids and moths	National, 30+ years
Institute of Terrestrial Ecology	Butterflies	National, 20+ years
Institute of Freshwater Ecology	Fish, plankton and alderflies	Local, 30+ years
Sir Alister Hardy Foundation for Ocean Science	Plankton	North Sea and North Atlantic, 50+ years
Coastal bird observatories	Migrant birds	National, 40+ years
County bird reports	Migrant birds	National, 90+ years
Horticulture Research International	Aphids and flies	Local, up to 30 years
	Apple, pear, narcissus flowering	Local, up to 30 years
British Naturalist Association	Various	National, varying durations from 1905
Private individuals	Herbs, trees, birds and amphibians	Local, varying durations from 1736
Royal Meteorological Society	Various	National, 1875–1947

(Online: Table I)

These findings on the relative changes in phenology of budburst and insect egg hatch have come from experimental manipulation and modelling. Long-term ecological data sets would enable empirical validation of the predictions. Leafing in oak has been monitored using long-term datasets published only very recently covering 167 years (Ref. 23) and 41 years (Ref. 24). Leafing advances by about six days for every degree celsius increase in mean temperature from January to March, in line with the model of Nizinski and Saugier[15]. Unfortunately, equivalent datasets do not exist for egg hatching in winter moth.

A good example of the use of long-term datasets to study synchronization between a herbivore and its host plant comes from a new analysis of phenological data over a 65 year period from 1883 to 1947 (Ref. 25). Remarkably similar trends were found in mean date of first appearance of the orange tip butterfly (Anthocharis cardamines) and first flowering dates of one of its host plants, garlic mustard (Alliaria petiolata), in relation to March temperature (Fig. 2) – loss of synchronization as a result of increasing temperature is therefore unlikely. Long-term phenological datasets also exist for various birds, amphibians, fish, plankton, insects, trees and other plants (Box 1), but there are few cases where these have been analysed comparatively for organisms interacting at different trophic levels, notable exceptions being for interactions involving freshwater[26] and marine[27,28] plankton.

Effects of climate change on spatial associations

Climatic warming has the potential to affect the spatial, as well as the temporal, coincidence of organisms[2,30]. The fossil record shows considerable instability in spatial associations between species from a range of taxa[2], and modern assemblages have no long-term history in the Quaternary[31]. The reason for the flux probably centres on the improbability of any two species sharing an identical set of environmental requirements and responses to given combinations of biotic and abiotic factors.

Recent modelling of the effects of increased temperature on the European corn borer moth (Ostrinia nubilalis) shows its potential for a northward range expansion throughout Europe of between 165 and 500 km for each 1°C rise in temperature[32]. To achieve this, its main crop host, grain maize (Zea mays), would also need to move. A 1°C rise in temperature is expected within the next 25 years[33], which means that to track this change as it happens, the moth would need to move between 6 and 20 km per year. Most insect species are able to migrate quickly enough to track changing environments[2], so an important constraint to range expansion in herbivores might be the rate of movement by their host plants. In the case of grain maize and other crops, such a natural constraint does not operate because the movement is achieved by man's intervention.

Models of crop–pest interactions are generally not climate driven and offer only limited prospects for predicting the impacts of climatic warming. Thus, empirical approaches will play a valuable role[34]. A recent generic package, 'CLIMEX' (Ref. 34), makes use of known associations between climate and species distributions, as well as information on species responses to climate. The background data are spatially rather than temporally extensive, so that future distributions are predicted on the basis of correlations between climate and current distributions over a wide area, rather than historical distributions over a small area.

In a new study, artificial temperature clines have been used to examine the effect of climatic warming on the outcome of competition between three species of fruit fly (Drosophila spp.) in the presence or absence of a parasitoid[30]. The ratios of the Drosophila species differed in different temperature clines and also according to whether the parasitoid was present, experimentally demonstrating the need to take into account the effect of climate on species interactions when predicting distributions. The distributions predicted by CLIMEX and related approaches therefore require that the expected species interactions are already happening in some part of the existing range and are hence built into the observed climate envelope.

Historical maps of forest type, defoliation frequency and climate have recently been used to assess the potential effects of climatic change on the western-spruce budworm-moth (*Choristoneura occidentalis*) and the gypsy moth (*Lymantria dispar*)[35]. With an increase in temperature alone, the predicted distribution of defoliation increases slightly for gypsy moth and decreases for the budworm. With an increase in temperature and rainfall, the predicted area of defoliation increases for both species, but with increased temperature and decreased rainfall it decreases. The results are due to changes in the distribution of the moths and of susceptible forest. However, these effects are not separated, because historical records of defoliation, not of moth species or tree species, were correlated with meteorological records as the basis for the predictions.

Research priorities

We have highlighted two distinct approaches to studying the impacts of climate warming on trophic interactions. One is to examine relationships between long-term or spatially extensive biological datasets and abiotic data, usually meteorological, available over a similar scale. The value of elements of the biological datasets are the result of all the interactions between components of the environment. This approach can lead to problems because future environments will include novel combinations of values of variables not encountered in the datasets used to analyse present relationships. A contrasting approach is to model interactions on the basis of experimentation that includes novel conditions expected in the future. Here, a problem is the enormous number of interactions and the difficulty of predicting which warrant most attention.

We suggest that the following research questions should be given priority:

• How do responses to temperature and CO_2 interact to affect phenology and distribution?

• What is the relative speed of adaptation to climate change, either through movement of appropriate genotypes or evolution of appropriate phenological cues, at different trophic levels?

• Can functional groups of organisms be defined on the basis of their responses to environmental variables and can these groups be used to predict the likely degree of dissociation of current community structure under predicted environmental conditions?

• How will changes in synchronization affect population dynamics?

There is no perfect way to examine these complex questions with the limited resources currently available. Prognoses based on the 'balance of evidence' from a range of approaches might eventually enable some generalizations to be made, just as they have been in relation to climatic change itself. Progress will be made if research groups using a particular methodology view alternative approaches as complementary rather than competitive. International collaborations such as the Global Change and Terrestrial Ecosystems project of the International Geosphere and Biosphere Programme are doing much to engender the right spirit.

Finally, it is important to stress the need for maintenance of long-term meteorological and biological datasets to validate predictions.

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Diversity in mimicry

Joron and Mallet's recent perspective in *TREE*[1] gives a good overview of current thinking on the evolution of mimicry, but in spite of an acknowledgement that mimicry has evolved in a wide range of organisms, the discussion was confined to butterflies. There is much recent work on other mimetic animals ranging from coral snakes[2] to spiders[3,4]. The article was unfortunately written before publication of a recent paper by McDougall and Dawkins[5] who show that when predator discrimination is introduced into behavioural models similar to those used by Speed[6], the results obtained are very different. These authors show that the criterion used in deciding whether a mimic is Müllerian or Batesian should not be palatability but the benefit that the mimic gains: if only one species benefits from the resemblance and the other loses, then the mimicry is Batesian, but where both species benefit, then the mimicry is Müllerian.

Butterflies are unusual among mimetic animals in that very often only the female is mimetic, and it is the female that is heterogametic. Furthermore, butterflies are unusual among Lepidoptera in being diurnal. Most Lepidoptera are nocturnal and relatively palatable to insectivorous predators, so it is mainly those taxa that are chemically protected and aposematic that have been able to escape the restrictions imposed by a nocturnal lifestyle (e.g. Zygaenidae and Ctenuchidae, as well as butterflies). This might help explain why butterflies that were originally thought to be Batesian mimics have now been shown to be unpalatable[7]. A comparable spectrum of palatability does not occur in many other mimetic taxa, such as the Araneae and Diptera. A great many syrphid Diptera are mimetic but none has been shown to be unpalatable[8], so these would seem to be Batesian mimics. The models are all well protected Hymenoptera, some of which are Müllerian mimics.

Because of this clear-cut difference between Batesian mimics and models, there is less advantage to a wasp or a bumblebee in embarking on an evolutionary chase to evolve away from their mimics than there is to

butterflies. As with mimetic butterflies, most syrphids are monomorphic, but there are several polymorphic species mimicking bumblebees in the genera *Merodon*, *Eristalis*, *Volucella* and *Criorhina*[9]. If the genetic-architecture problems involved in the evolution of such polymorphisms are as great as implied by Joron and Mallet, then, because so many mimetic species are polymorphic, the advantages of polymorphism must be very substantial.

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Joron and Mallet's recent *TREE* perspective on diversity in mimicry[1] oversimplifies our views[2] on anomalous pattern polymorphisms in the African Queen butterfly, *Danaus chrysippus*. We did not explain these anomalies by an overload of Batesian mimics; rather, we discussed this possibility in the context of hybridization between previously allopatric colour pattern races of this species. We agree with Joron and Mallet's objections to the overload hypothesis (and would add a third), but we note that they apply more to the origin of a polymorphism than to its maintenance. In a hybridization context, theory suggests that Batesian overload can contribute to polymorphism dynamics.

Because the polymorphism of *D. chrysippus* is so interesting, it is often forgotten that this species is actually monomorphic over most of its range in Africa. Pattern polymorphism is restricted to east and central Africa, albeit in an area larger than Europe[3]. It is unlikely that special conditions (e.g. lower deterrence leading to Speedian mimicry[4,5]) prevail here but not in the rest of Africa. Given that it is in east and central Africa that the different colour pattern morphs of *D. chrysippus* overlap in their geographical distributions, Occam's razor suggests a hybrid origin for the

polymorphism. This interpretation is supported by independent evidence from segregation anomalies for sex and colour pattern[3], large scale migrations[6], assortative mating[7,8] and heterosis for body size[9]. Polymorphism dynamics are highly complex, and they are most definitely not determined by predation alone.

The take-home message from all this is that mimicry and aposematism are not the whole story. Predictions from the theory of mimicry and aposematism depend not only on accurate modelling of predator behaviour and prey characteristics, but also on several other things being equal. In particular, they assume that predation determines the frequencies of colour pattern genes without interference from other selection pressures, ecological circumstances or other loci. This *ceteris paribus* clause can be generalized as an extreme form of beanbag genetics, in which there is optimal, independent tracking by individual loci of contemporary selection pressures. In reality, genes for mimetic colour patterns are the products of complex and particular processes, in which various selection pressures (not just predation) and historical contingencies may be important. Colour pattern genes may also