Review

Autumn, the neglected season in climate change research

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Autumn remains a relatively neglected season in climate change research in temperate and arctic ecosystems. This neglect occurs despite the importance of autumn events, including leaf senescence, fruit ripening, bird and insect migration, and induction of hibernation and diapause. Changes in autumn phenology alter the reproductive capacity of individuals, exacerbate invasions, allow pathogen amplification and higher disease-transmission rates, reshuffle natural enemy–prey dynamics, shift the ecological dynamics among interacting species, and affect the net productivity of ecosystems. We synthesize some of our existing understanding of autumn phenology and identify five areas ripe for future climate change research. We provide recommendations to address common pitfalls in autumnal research as well as to support the conservation and management of vulnerable ecosystems and taxa.

The neglect of autumn

Numerous effects of climate change on the spring phenology (see Glossary) of temperate plants and animals are well documented [1,2]. Warmer temperatures have resulted in earlier leaf-out and flowering of plants, earlier arrivals of migratory songbirds, and earlier emergence and spring migration of insects [3,4]. Autumn, by contrast, has received less attention: in the publication database Scopus there are only about one-half to one-third as many climate change studies set in autumn as compared to spring (Table 1). The neglect of autumn in phenology and climate change research is likely caused by a combination of factors, including the complexity of drivers of autumn phenology, the protracted nature of autumn events, and human enchantment with the sudden burst of spring flowers and wildlife following winter.

Despite this relative neglect, autumn events are also hugely important ecologically and evolutionarily. They signal the end of the growing and breeding season for most temperate and arctic plant and animal species, and are an understudied component of the ecological impacts of climate change. In the following review we synthesize some of our existing understanding of autumn phenology, identify five areas ripe for future research, and provide recommendations for research in those areas.

What we know about autumn

In temperate ecosystems, the autumn phenomena that have received the most attention in climate change research are leaf senescence and migratory bird departures. Insect diapause and fruit ripening have also garnered moderate interest. Other autumn phenomena such as amphibian dormancy and bud formation remain less studied and poorly understood.

Despite the relative neglect of autumn, ecologists have made important progress in understanding the drivers of autumn phenology and the effects of climate change on autumn events (Figure 1). Long-term observational datasets indicate that leaf senescence is, on average, delayed by increasing temperatures [4,5]. In addition, community- and landscape-level studies show that invasive non-native plants can gain an advantage over native species by extending their growing seasons in autumn [6], and that an extended growing season allows many perennials to sequester more carbon – which in turn alters local climate and ecosystems [7]. Long-term data indicate that birds are shifting their autumn phenology in response to climate change, with short-distance migrants generally delaying migration and some long-distance migrants leaving earlier [8–10]. Insects that have been examined have responded to

Glossary

Autumn migration: the annual long-distance movement of individuals from their breeding ground to their wintering ground. In the northern hemisphere, autumn migrants typically fly north to south. Many temperate- and arctic-breeding birds migrate in autumn, as do insects such as monarch butterflies and some dragonflies.

Diapause: a physiological state of dormancy. In arctic and temperate ecosystems, diapause is a hormonally driven hiatus in developmental or reproductive processes. Diapause can occur in any life-stage, and is an important overwintering strategy for insects and other animals.

Leaf senescence: leaf aging, resulting in a decline in function, that in temperate regions is associated with seasonal leaf-color change and leaf drop. Plants reabsorb essential nutrients from their leaves before autumn leaf senescence.

Net ecosystem productivity (NEP): for an ecosystem, the balance between carbon sequestered through photosynthesis and the carbon lost through respiration. Warming autumn temperatures can delay leaf senescence and extend photosynthesis and the growing season, but can also disproportionately increase ecosystem respiration.

Phenology: the timing of seasonal biological events. Spring events including flowering, leaf-out, and insect emergence have been shown to advance in response to warming temperatures. Autumn events such as leaf senescence and autumn migration are less well studied, but are often delayed by a warming climate.

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Table 1. Autumn has received less attention than spring in the climate change literature[a]

'Climate Change'	'Autumn'	'Spring'	Autumn (%)
Climate Change (CC)	3248	8751	27.1
'Leaf*' and 'CC'	212	549	27.9
'Bird*' and 'CC'	100	413	19.5
'Insect*' and 'CC'	73	188	28.0
'Fruit*' and 'CC'	63	–	15.4
'Flower*' and 'CC'	–	346	
'Mammal*' and 'CC'	39	108	26.5
'Amphibian*' and 'CC'	7	32	17.9

[a]Results from a Scopus search conducted on December 11, 2014. The first search included 'climate change' (CC) and either 'autumn' or 'spring' (the terms 'fall', 'autumnal', and 'autumn*' yielded many false hits, whereas the terms 'spring' and 'autumn' yielded a large fraction of relevant titles and abstracts). Each subsequent search included 'climate change', as well as either 'autumn' or 'spring' and a taxon/plant organ search term, as listed in the left-hand column of the table (the asterisk represents the truncation/wildcard term). Results include the number of publications returned for all years. Autumn (%) indicates the percentage of the total citations for each taxon that include autumn in title, keywords, or abstract. The percentage for fruit is based on the combined fruit and flower total.

warmer autumn temperatures with faster developmental rates, added generations, and delayed migration and diapause [11,12]. Fruit ripening of native plants, by contrast, is the only autumn event of which we are aware to have advanced, on average, in response to warming temperatures [4,13]. As we will describe, changes in autumn phenology can also increase the reproductive capacity of individuals, exacerbate invasions, alter the ecological dynamics among interacting species, and affect the net productivity of ecosystems.

Drivers of autumn phenology

While various measurements of spring temperature can explain most of the variation in leafing-out times [14], autumn senescence is more weakly linked to autumn temperatures [15] (Figure 2), as well as to the combination of temperature and photoperiod [7,16]. Other less-predictable factors can explain additional variation; for example, drought can advance leaf coloring and leaf drop while abundant soil moisture can delay senescence [17]. Early frost events and high winds can also result in sudden leaf senescence and abscission [18,19]. Air pollution in the form of tropospheric ozone can induce early senescence, while local CO_2 concentration has been reported to have no effect [18,20].

Insect diapause and migration phenology also vary substantially among species and are often modeled as a combination of photoperiod and temperature [21]. Although most temperate insect species appear to rely in part on photoperiod controls to induce diapause, some species such as the parasitoid wasp *Leptopilina japonica* and the European corn borer (*Ostrinia nubilalis*) enter diapause in response to minimum temperatures or daily temperature cycles alone [22,23]. For autumn-migrating insects, migration timing is also usually driven by day length and temperature, but it can also be affected by rainfall, humidity, host plant senescence, and wind [12,24].

The timing of autumn bird migration is driven by many factors, and species-specific interactions among factors, including environmental conditions (e.g., temperature and photoperiod), life-history traits (e.g., broodedness and wintering location), spring arrival times, migration

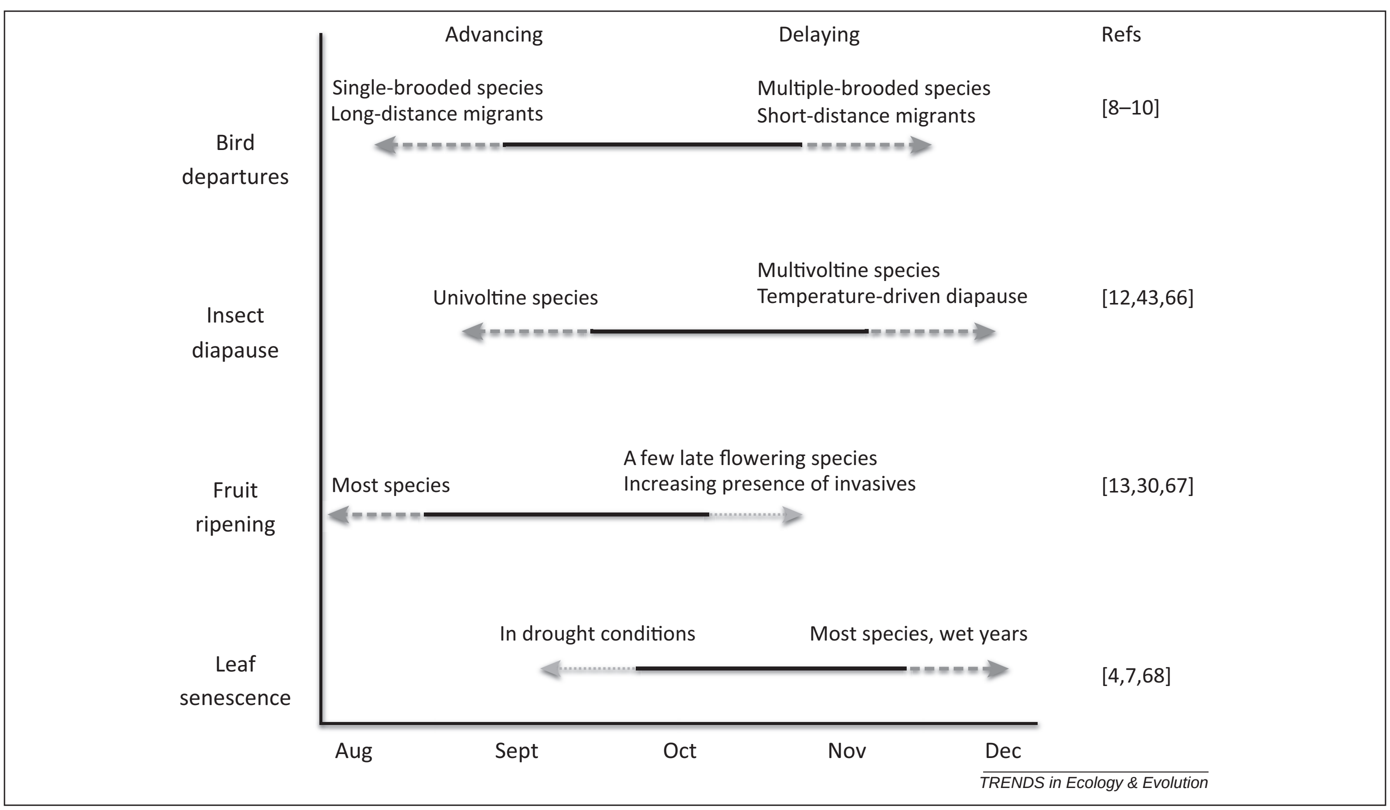

Figure 1. Expected phenological shifts of autumn events in response to climate change. We indicate how leaf senescence, bird departures, fruit ripening, and insect diapause are expected to respond to climate change in temperate ecosystems of eastern North America. Gray broken lines indicate the direction in which an event will shift; darker stippling indicates a response that is common, while lighter stippling indicates a response that is comparatively rare. Some of these changes are happening already. The data for leaf senescence and bird migration are most complete, while there is far less information on fruit maturation times and insect diapause. [4,7–10,12,13,30,43,66–68]

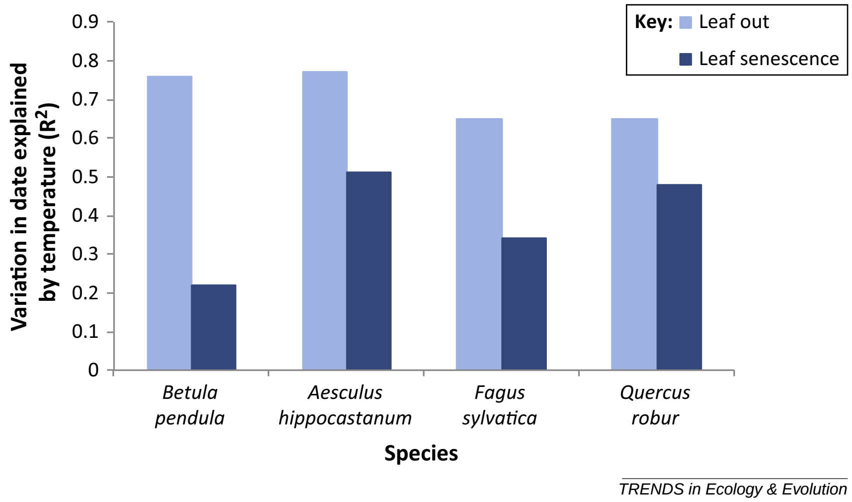

Figure 2. Temperature explains more variation in spring than in autumn leaf phenology. Correlation coefficients (R^2) between event date and the preceding mean monthly spring and autumn temperatures for four tree species in Germany (1951–2000). Data from [15].

speed, and endogenous circannual rhythms. The proportional influence of these drivers varies widely among species, migratory cohorts, and geographies [8–10,25,26], and requires further, widespread investigation using multivariate analyses.

Methods for studying autumn phenology

Compared to those that take place in the spring, observational studies of autumn phenology are faced with greater methodological challenges, such as defining events, standardizing methodologies, and treating autumn phenomena as multiple-day events. It is apparent that many autumn studies, for example those of leaf senescence and fruit maturation, are based on somewhat subjective observations such as '50% leaf fall' or descriptions of fruit colors [4,27]. In addition, most researchers do not adequately describe their methods, making it difficult to compare records across studies.

One challenge for defining autumn events is that although spring events such as leaf-out and insect emergence are sudden and visually apparent, autumn events such as leaf senescence, fruit ripening, and bird and butterfly migration are protracted and asynchronous. Definitions of leaf-out in spring are similar, and occur within days of one another; by contrast, definitions for the date of senescence range from the date of first leaves changing color to the date of 100% abscission — events that can occur weeks apart [28,29]. Autumn bird migration is also temporally extended, and can involve multiple waves of migrating birds [3]. Fruits typically mature over an extended period as well, as part of their reproductive and dispersal strategy, which contrasts with the sudden and brief flowering-window for many species [30]. Thus, it is not possible to assign single dates to many autumn phenomena. It is also more difficult to observe the last date of activity for a species in the autumn than the date of its first appearance in spring because absence can be more challenging to observe than presence, and, in the case of birds, autumn behavior is less conspicuous [3].

It is clear from the recent autumn literature that researchers will have to deviate from spring methodology to appropriately capture autumn events. Autumn definitions must be biologically relevant and comparable across studies, and this could require treating autumn phenomena as multiple-day events [31].

The influence of autumn on carbon storage

Autumn phenology plays an important role in the annual carbon balance of temperate ecosystems. Later senescence dates contribute to longer growing seasons in temperate and arctic regions [32]. Wu *et al.* [33] found that changes in autumn leaf phenology in temperate forests better explain variation in annual net ecosystem productivity (NEP) – in other words, the balance between photosynthesis and respiration – than do changes in spring phenology. Delayed autumn leaf senescence is associated with increased NEP, meaning that ecosystems tend to sequester more carbon in warmer years with later autumn phenology [7,34,35]. However, this result is not universal; autumn warming also elevates ecosystem respiration, occasionally outweighing increased autumn production, which can turn current carbon sinks into future CO_2 sources [36].

The variety of factors affecting autumn NEP complicates attempts to forecast the implications of longer growing seasons on NEP. At the Harvard Forest in Massachusetts, spring ecosystem respiration is dominated by respiring foliage, but autumn respiration is dominated by below-ground root and microbial respiration [37]. Furthermore, although they are often lumped together as 'soil respiration', root and microbial respiration differ in their responses to environmental change [38]. The phenology of roots and microbial activity is poorly understood, and observations suggest substantial variability in root phenology of temperate tree species [39]. In addition, root phenology cannot be determined from above-ground plant phenology [40]. The lack of data regarding the partitioning of above-ground, root, and soil microbial phenological responses to climate change remains a large limitation in our understanding of, and ability to forecast, how autumn climate change will influence carbon sequestration. Given the magnitude and importance of above- and below-ground arctic and temperate carbon resources, the need for more ecosystem-level studies and models addressing autumnal phenomena remains great.

Invasive species, pests, and pathogens in autumn

Phenotypic plasticity and rapid evolution allow some invasive species to be more responsive to warmer autumn temperatures and later freezing events than are many native species [41]. Fridley [6] found that many non-native invasive shrub species in the eastern USA gained an advantage of greater autumn carbon assimilation over native shrub species through delayed leaf senescence in autumn, rather than via earlier leaf-out in the spring (Figure 3). Thus, the lengthening growing season likely contributes to the advantage some invasive species, such as Morrow's honeysuckle (*Lonicera morrowii*) and Glossy buckthorn (*Rhamnus frangula*), have over many native shrubs, and might be considered as a bet-hedging strategy to maintain viable leaves despite the increasing risk of frost damage.

Warmer autumn temperatures also present an advantage for some insect pests. By speeding development and delaying diapause, many insects produce more generations in warmer, longer growing seasons [42]. The diapause of Spruce beetles (*Dendroctonus rufipennis*) and Douglas fir beetles (*Dendroctonus pseudotsugae*), for instance, can be either disrupted or delayed with warmer autumn temperatures, extending both reproductive capacity and feeding activity [43]. Already, warmer autumn and winter weather has allowed bark beetle populations to increase and has magnified damage to trees in the western USA and Canada.

There are consequences for human health as well. Warmer autumns have led to extended autumn activity of ticks and mosquitoes [44,45]. Ticks (e.g., *Ixodes* species) continue to search for blood meals in autumn as long as temperatures remain above their activity thresholds, and have the potential to infect people with Lyme disease [46]. Delayed onset of winter allows amplification of both mosquito populations and their viruses [47]: human infections of West Nile virus are much more prevalent in the fall, and some mosquito vectors are known to take a larger fraction of their blood meals from mammals in the fall following the departure of migratory birds [48]. Similarly, wildlife such as caribou (*Rangifer tarandus*) are expected to experience a longer infective season by the nematode *Ostertagia gruehneri* with warmer temperatures in the spring and autumn, thus increasing their likelihood of infection [49] (Figure 4).

Much published literature focuses on invasive species, pests, and pathogens that stand to benefit from climate change. Certainly, there will also be disadvantaged invasive species, pests, and pathogens. For instance, while some insect pests experience faster development times and increased generations, others respond to increased temperatures (those beyond their optimum range) with slower development times, lowered reproductive capacity, and increased mortality [50]. Many sap-feeding insects respond to water-stressed host plants and decreased humidity with shorter lifespans, lowered fecundity, and elevated dispersal rates [51,52]. We also expect within-species regional variation in the effects of climate change on autumn insect abundance based on temperature thresholds and range shifts. For instance, although native ash trees (*Fraxinus* sp.) in the northern USA are expected to experience heightened herbivory from the introduced emerald ash borer (*Agrilus planipennis*), trees that occur at lower latitudes are predicted to experience decreased herbivory from the beetle [53].

Interspecies interactions

Species rely on synchrony for interspecific interactions in autumn, exactly as they do in spring and other seasons. Some insects lay their eggs on particular fruits, birds consume particular types of fruit during migration, and

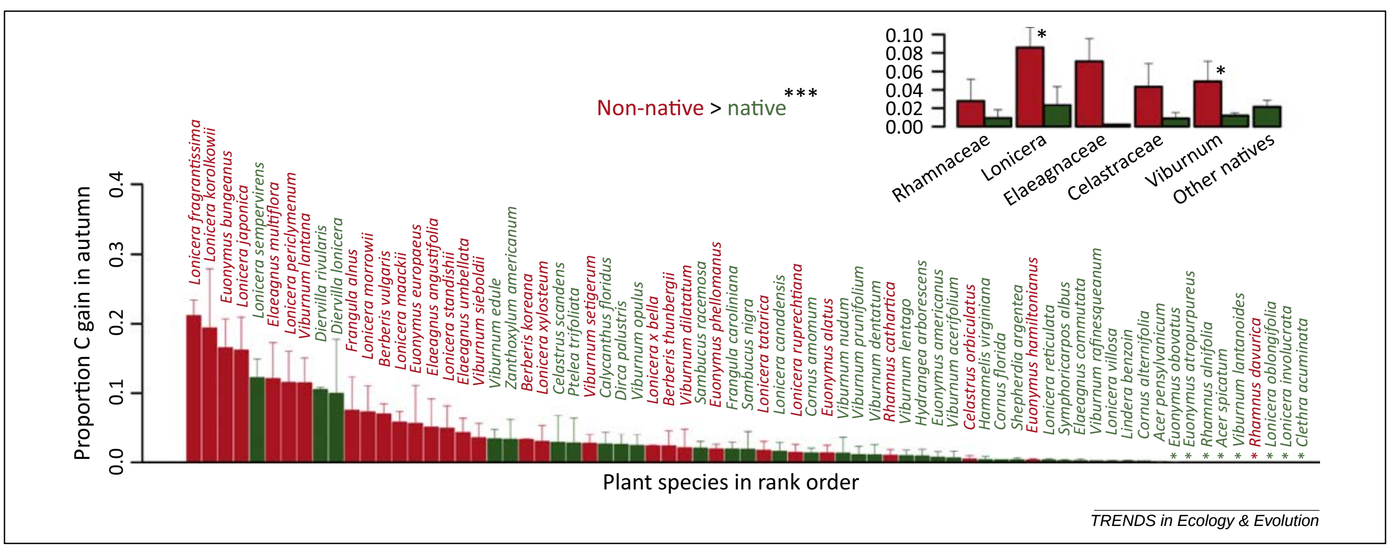

Figure 3. Non-native invasive plants gain an advantage over native species with extended autumnal growth. Mean proportions (with standard errors) of seasonal carbon (C) assimilation (of total carbon assimilation) by native (green) and non-native (red) species (many of which are invasive) in autumn (after approximately 24 October). Many non-native species are better able to assimilate carbon in the autumn, and extend their growing season in comparison with native species. Colored asterisks on the bottom right reflect autumn carbon gain of less than 0.5%. The inset depicts comparisons between native and non-native members of different phylogenetic groups, with asterisks denoting the significance of comparisons (*, $P<0.05$; ***, $P<0.001$). Reproduced from [6].

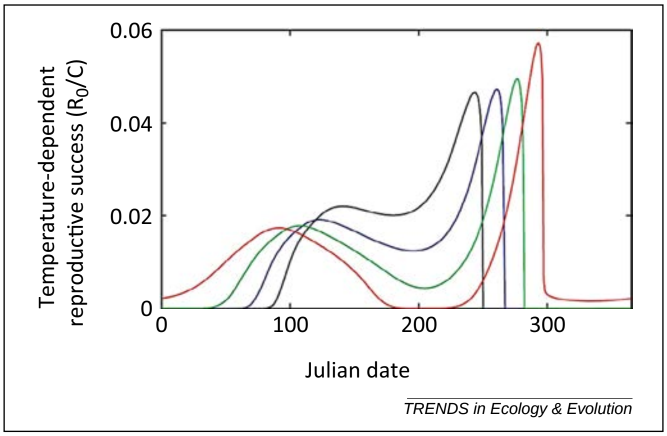

Figure 4. A warming climate will extend the infective period of the nematode (*Ostertagia gruehneri*), which causes disease in the caribou (*Rangifer tarandus*). In four seasonal climate scenarios, with black, blue, green, and red representing successively warmer climates, the temperature-dependent reproductive success of the nematode (indicated by the index R_o/C) is predicted by a model to start earlier in the year and extend later in the year as conditions warm. Nematode reproductive success, and its resulting ability to infect hosts, declines in summer as a result of the decreased ability of the nematode to survive hot weather. Reproduced from [49].

many specialist insect folivores feed into autumn [12,30,54]. Asynchrony can result when interacting species experience different magnitudes or directions of phenological shift in response to climate change. In spring, climate change has resulted in asynchrony between herbivores and leaves, flowers, and pollinators, and between migratory birds and their insect prey, in some cases leading to decreases in survival and reproductive success [55–57]. The variability of temporal shifts in autumn also creates possibilities for asynchrony, but these remain little studied.

Songbirds primarily consume fruits during autumn migration, and many plants rely on birds to disperse their seeds [30]. However, climate change is advancing fruit-ripening dates and delaying songbird departures for many species [4,10]. This mismatch will change songbird diets, particularly for those short-distance migrants that depart late in the season. Invasive non-native plants often produce abundant fruits of low nutritional quality that last later into the autumn season [30,58]. Because many songbirds delay departures as a consequence of a warming climate, they will likely feed more on the fruits of invasive species, increasing invasive seed dispersal.

The possibility of mismatches involving insects is both intriguing and largely unknown. Because invertebrates often have short generation times and large brood sizes, most have great capacity for tracking climate changes. Monophagous insects that feed on developing seeds and fruit might experience changing food resources if climate change affects their developmental timing. Additional broods will extend the presence of some species, exposing them to new complexes of predators, parasitoids, and pathogens. The tachinid fly *Compsilura concinnata*, introduced into North America from Europe to control gypsy moth [59], is now successfully producing an additional fall generation in New England (Jeff Boettner, personal communication), which parasitizes late-season notodontid moth caterpillars and other non-target species. Almost all the studies documenting asynchrony between parasitoid insects and their hosts have been conducted in the spring when emergence asynchrony can be dramatic. The more subtle appearance of autumn phenomena does not mean that they have smaller effects on population dynamics – rather it means that much further study in this area is warranted.

Even within a taxon the consequences of climate change are complex and are likely to have both positive and negative effects. Taking the Monarch butterfly as an example, several studies have warned that climate change threatens the overwintering roosts in Mexico [60], and there is mounting evidence that droughts in the south-central and southwestern USA have contributed to the butterfly's recent demographic collapse across eastern North America [61]. However, warmer average temperatures and prolonged autumnal conditions are favorable to larval development, and will shift the milkweed range to make more plants available to Monarchs in Canada and the northern USA [62].

The future of autumn research

Based on what is already known about autumn events, and the conspicuous gaps in our overall understanding on the topic, we make five core recommendations for future research into the effects of climate change on autumn phenology.

(i) Researchers should use factorial experiments and large-scale, multispecies observational studies to determine the mechanisms affecting autumn events, as well as the underlying phylogenetic signals. Information on the factors controlling autumn events currently comes almost entirely from small-scale observational studies. Experiments that test the effects and interactions of factors – such as temperature, soil moisture, frost events, host-plant quality, and photoperiod – will make it possible to isolate and quantify the drivers of leaf senescence, fruit ripening, and insect diapause. Similarly, large-scale, multispecies studies will help to quantify the role of shared evolutionary history of closely related species in influencing fall phenology. The findings that experimental warming studies underpredict the influence of temperature on spring phenology, and that phenology is often phylogenetically conserved, reinforce the importance of isolating drivers experimentally, accounting for phylogeny, and of comparing experimental findings to long-term observational studies [1,63–65].

(ii) Autumn events should be methodologically and statistically treated as multiple-day events rather than single dates, and definitions should be standardized where possible. We encourage researchers to treat autumn events as multiple-day events, recording the beginning, duration, and end of autumn phenomena, and analyzing changes in each of these three response variables [31]. This approach avoids the challenge of developing robust single-day definitions for each autumn event, and more accurately reflects ecological reality. Where possible, researchers should aim to record metrics – such as chlorophyll content or coloration – on a continuous scale, making it possible to then determine rates of senescence, points of inflection in the season, or the timing of markers such as 50% change [7].

Future research should prioritize the development and standardization of common empirical techniques and definitions, such as those developed by the USA National Phenology Network [31], for the sake of spatial and temporal comparisons. Leaf senescence observations could be standardized through the use of handheld chlorophyll meters and leaf litter measurements, and fruit-ripening dates could be standardized with reference color samples and sugar content measured with a refractometer. Emerging technologies should be applied to standardizing autumn phenology measurements: smartphone apps for citizen scientists can enhance the spatial resolution of phenological observations, while geolocator tags and GPS tracking devices can be used to monitor the departures of inconspicuous migratory birds with improved accuracy and detail.

(iii) Further research should examine the separate effects of climate change on the phenologies of above-ground, root, and microbial respiration, and assess the effects of changes in autumn phenology on the cycling of carbon and other key nutrients. Models that account for the differential changes in above-ground, root, and microbial respiration are necessary for reasonable forecasts of the effects of climate change on NEP and the cycling of carbon and nutrients. These components will be most easily differentiated by experiments examining the effects of warmer, drier autumns on the magnitude and phenology of root and microbe respiration below ground, as well as above-ground respiration of leaves and wood. The dominance of autumn below-ground respiration in carbon losses makes separating root and microbial respiration, and measuring widely across the temperate landscape, important next steps for reducing error in carbon cycling models. The Keenan *et al.* [35] method of combining satellite data, biosphere models, and ecosystem-level carbon flux measurements with long-term field observations is an excellent example of synthesizing approaches to investigate the effects of climate change on NEP. Expanding such methodologies will allow better worldwide projections of carbon balance and feedbacks to climate change in autumn.

(iv) Researchers should investigate the role of autumn climate change on the success of pests, pathogens, and invasive species, and the importance of these findings for recommended management practices. Given the disproportionate influence of pests, pathogens, and invasive species on ecosystems and society, forecasts of the effects of climate change and phenological changes must take these factors into account [49]. Moreover, given the success of particular invasive plant species and pests in the autumn, conservation agencies might need to adjust how they identify which species are of the highest priority to manage. For effective management of these groups and their ecological communities, researchers should identify the features (e.g., origin site, feeding strategy, minimum temperature optimum) common to invasive species, pests, and pathogens that benefit from autumn climate change, as well as how changes to these groups impact upon species in the surrounding community.

(v) Finally, autumn phenology changes have the potential to result in ecological mismatches and dietary changes among interacting species; priority should be given to studying species, such as specialists and migrants, that are particularly vulnerable to environmental change. With many long-distance migrant bird and insect species already in decline due to loss of breeding, wintering, and stopover habitat, as well as other threats, mismatches for long-distance migrants should receive special attention. These mismatches are not limited to the complete loss of interactions – instead they can alter the quality of interactions, such as effects on the abundance or nutritional quality of food, or on the strength of competitive or mutualistic interactions [55,56]. Adaptive plasticity will serve to mitigate some phenological mismatch through individual adjustments. However, mismatches will likely still take effect at the community scale. Future studies should aim to explore these relatively subtle effects of phenological changes on the quality of food and other factors, particularly for specialized and otherwise vulnerable groups, such as long-distance bird and insect migrants, organisms with complex cycles, and species with small effective population sizes. Thus, research in these areas will inform management recommendations that can help to protect key interactions for rare and otherwise imperiled species.

While we have focused here on five important research areas, there are other gaps in our knowledge of how climate change impacts on autumnal phenomena. Remarkably few studies have followed the carry-over impacts of autumnal conditions on the following spring or followed individuals across multiple years. Another exciting topic in much need of study is the extent to which autumn responses to climate change are genetic versus plastic. Do autumnal responses have more plasticity built into them than their vernal counterparts? We have the sense that organisms do more bet-hedging in the fall, perhaps because the fitness consequences for encountering frost are lower in autumn than in the spring – and, if so, what are the underlying mechanisms that allow such plasticity in response?

Conclusions

Research has identified many of the primary environmental drivers of autumn phenology. However, much uncertainty remains about the relative contributions of different drivers, how they interact with species' life-histories, and how temporal shifts will manifest at the community and ecosystem level. What we have outlined here are promising avenues for future research in autumn phenology, and possible implications for conservation management. This field remains wide open for discovery, particularly by way of experiments, mechanistic modeling, and observations of species interactions. We urge ecologists to study the effects of climate change and phenological changes in the autumn window – as very many studies have already accomplished for the spring.

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