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Forum

The Missing Angle: Ecosystem Consequences of Phenological Mismatch

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Climate change leads to unequal shifts in the phenology of interacting species, such as consumers and their resources, leading to potential phenological mismatches. While studies have investigated how phenological mismatch affects wild populations, we still lack studies and a framework for investigating how phenological mismatch affects ecosystems, particularly nutrient cycling.

Climate Change, Phenological Mismatch, and Nutrient Cycling

Shifts in the seasonal timing of recurring biological events (i.e., phenology) are among the most notable ecological responses to climate changes. In general, spring phenological events, such as reproduction and migration, are occurring earlier [1]. However, among-species variation in response to climate change has fueled concern that key interactions between species are becoming mismatched over time, with documented consequences for wild populations [1,2].

However, phenological mismatch is not developing in all situations and recent syntheses provide a framework for understanding when they are most likely to occur (e.g., [2]). For example, lower trophic levels and smaller-bodied organisms are more likely to keep up with changing climates. Furthermore, species in mutualistic relationships (i.e., plant–pollinator) appear more synchronized [3]. By contrast, antagonistic interactions (i.e., consumer–resource) appear most likely to realize diverging phenologies [3]. In addition, we are beginning to appreciate how two-species temporal disruptions can be felt beyond their direct interactions, and across communities and landscapes [4].

In fact, there have been numerous assertions that phenological mismatches may have ecosystem consequences [1,2,4], yet few studies focus on these consequences. Here, we highlight the importance of broadening the scope of phenological mismatch studies to include ecosystems and improve our understanding of global change impacts in terrestrial environments. While there are many ways to measure ecosystem responses to phenological mismatch, we focus on a supporting service, and, more specifically, the impacts on carbon (C) and nitrogen (N) cycling because of their importance in ecosystem productivity and climate feedbacks.

A Case Study: Sedge–Goose Mismatch

We conducted what we believe to be the only experiment designed to investigate how phenological changes influence ecosystem functioning, namely C and N cycling. The experiment focused on a developing mismatch between a sedge (*Carex subspathacea*) and Pacific black brant (*Branta bernicla nigricans*) in Alaska, USA. We found that, even though migratory geese are arriving earlier each year (a change beneficial to their populations), this change has adverse effects on primary producers and the ecosystem (Figure 1A). Earlier goose arrival reduces plant biomass, sexual reproduction, and possibly genetic diversity. This, in turn, increases soil N availability and potential N leaching, and shifts the system from being a summer-season C sink to a C source [5–7]. However, if geese are delayed, and the growing season comes earlier, we see the opposite responses (Figure 1B). This contrast illustrates how a simple change in the timing of herbivory, a trophic relationship typically focused on the impact to consumers, can have cascading ecosystem consequences and even climate feedbacks.

It was possible to conduct this experiment and have it produce meaningful predictions for the effects of phenological mismatch on nutrient cycling because: (i) we had long-term data sets on the phenology of both species; (ii) the phenologies of both species are influenced by climate change; (iii) the species have a strong interaction; and (iv) both species alter resource pools, so their asynchrony was bound to alter ecosystem functions, such as C uptake and N cycling. Over the 3 years we conducted this experiment, some variables changed the direction of their response to the timing of these species, suggesting that combining experiments with long-term data sets is critical [7].

Some Hypothetical Examples

Here, we provide other examples of potentially developing mismatches to

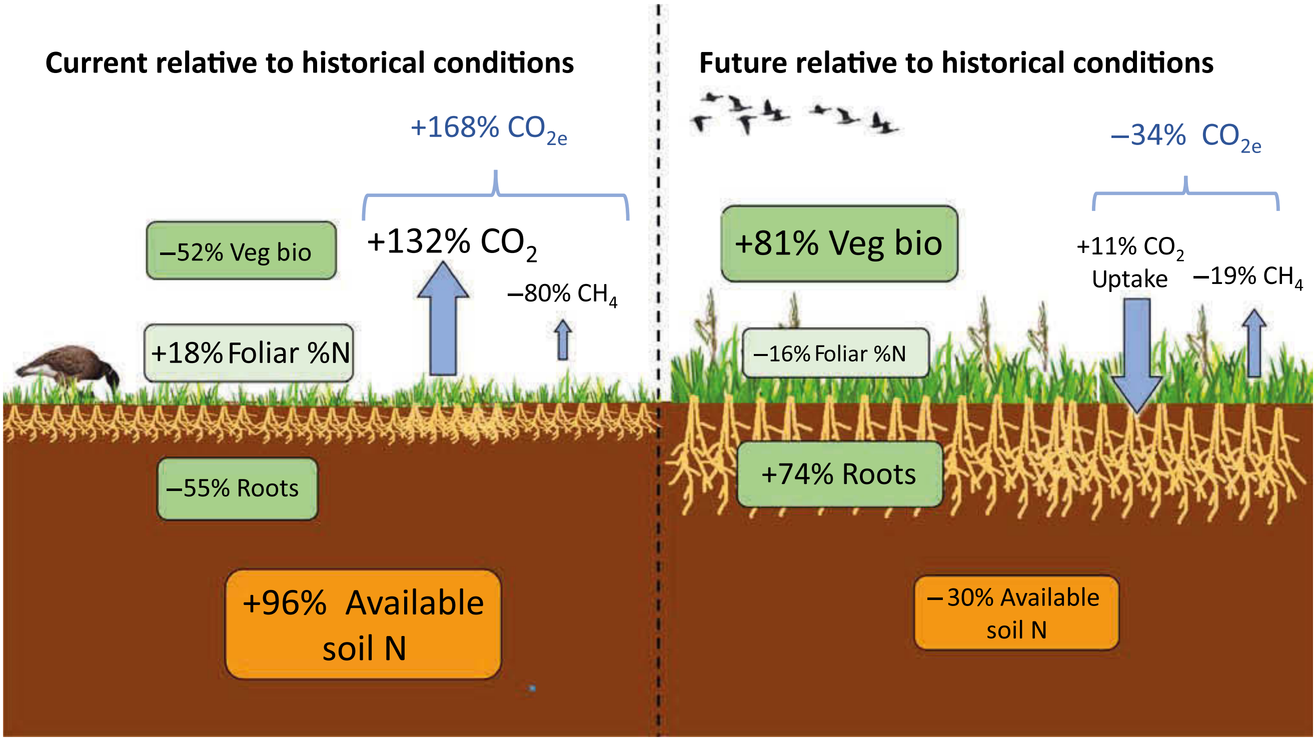

Figure 1. Ecosystem Consequences of Mismatch between Pacific Black Brant and Their Dominant Forage (Yukon-Kuskokwim Delta, Alaska, USA). We measured ecosystem responses to manipulated changes in the timing of both the growing season and arrival (grazing) by migratory geese. We compared both 'current' and 'future' climate scenarios with historical baseline conditions. (A) To reflect changes already underway, the 'current' scenario represents a natural springtime start date and an earlier than historical goose arrival time, which has occurred frequently in the past decade [5]. (B) The 'future' scenario includes an earlier springtime start date and a later than historical goose arrival time. This treatment was selected because we expect both spring to advance and geese to arrive later in the coming decades as environmental cues for migration from the wintering grounds diverge from those at the breeding grounds. In the current scenario, there is less above- and belowground biomass, higher quality goose forage, greater soil available nitrogen (N), and greater CO_{2e} (CO_2 equivalent greenhouse gas emissions). In the future, we expect an increase in above- and belowground biomass, a reduction in forage quality, less soil-available N, and greater CO_{2e} uptake even as CH_4 emissions increase [5–7]. While late goose arrival is worse for geese in terms of forage quality, it will result in greater C sequestration and lower greenhouse gas emissions.

illustrate how they may influence nutrient cycling, at least over the short-term (Figure 2).

Example A: Vegetation–Caribou Mismatch

Migratory caribou (*Rangifer tarandus*) arriving late to breeding areas in Greenland experience lower forage quality [8], but this mismatch may also have other ecosystem consequences. If caribou are delayed, longer periods of growth may result in greater plant biomass and stronger vegetation sinks for C and N.

Example B: Caterpillar–Bird Mismatch

If great tit (*Parus major*) migration to breeding grounds in western Europe does not match peak caterpillar biomass, it may be more than the chicks that are affected [9]. Increased caterpillar abundance early in the season could result in greater oak (*Quercus robur*) herbivory and decreased aboveground leaf biomass, reducing the C and N sink strength of these trees.

Example C: Salmon–Grizzly Mismatch

In Alaska, earlier emergence of elderberries (*Sambucus racemosa*) is causing grizzly bears (*Ursus arctos middendorffi*) to switch food sources away from salmon (*Oncorhynchus nerka*) early during the summer [10]. Delayed bear consumption of salmon could reduce available C and N in riparian and forest ecosystems, where salmon carcasses are an important source of nutrients.

Example D: Plant–Pollinator Mismatch

An important ecosystem service that phenological mismatch may affect is pollination of fruit-producing trees [11]. For example, if apple trees are not pollinated, then the C a tree would dedicate to fruit may be shunted to growth and storage, making the plant a greater C sink.

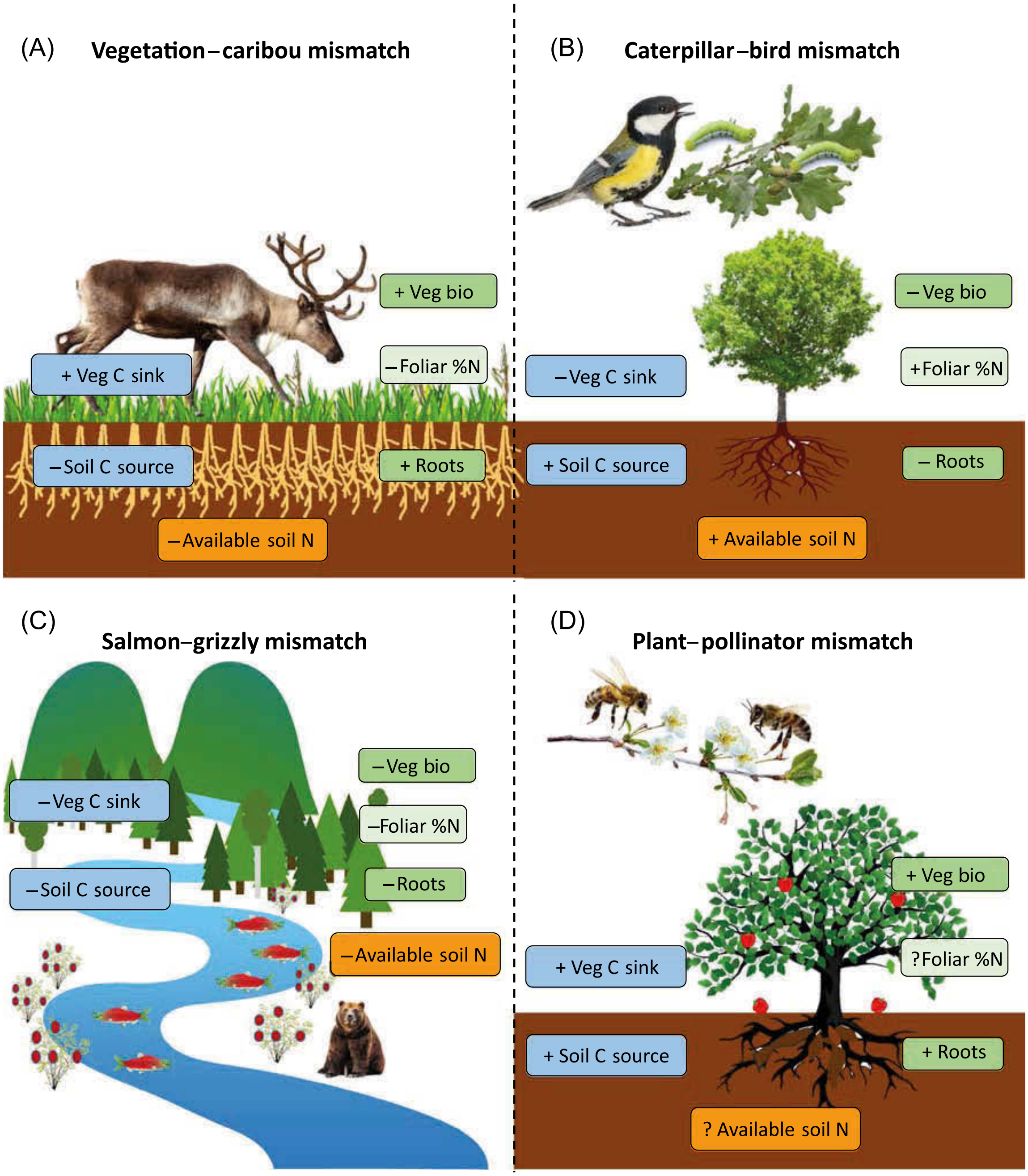

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Figure 2. Examples of Hypothetical Ecosystem Responses to Phenological Mismatches, Focusing on Consequences for Plant Biomass and Forage Quality, Carbon (C) Source and Sink Strength, and Nitrogen (N) Uptake and Cycling. In (A), delayed herbivory increases the C sink strength in vegetation, which increases N demand by plants. Delayed herbivory also means longer periods without N returned to soils as feces, slowing N cycling, and potentially limiting N availability. When caribou (*Rangifer tarandus*) arrive, they find leaf tissue of lower quality because the tissue is older and the N pool is diluted across more biomass. (B) mirrors (A), but at a higher trophic level. Here, lack of insectivorous birds increases herbivory, reduces C sink strength in the plant, and increases N availability in the soil. In (C), grizzly bears (*Ursus arctos middendorffi*) switch food sources in response to the earlier phenology of fruit. This reduces the transport and consumption of salmon, and plants lose a critical nutrient resource, reducing C sink strength, lowering forage quality, reducing soil microbe C, and slowing N cycling. In (D), lack of pollination due to mismatch reduces fruit set. The lack of fruit shifts the C pool in the ecosystem away from labile fruits and towards recalcitrant roots and shoots, and the increased fine root growth and rhizodeposition may result in greater soil respiration. Blue indicates C sink and sources, green indicates vegetation variables, orange indicates soil N, veg bio indicates aboveground plant biomass, and +/–/? indicate the hypothesized direction of the relationship.

Incorporating Ecosystem Consequences

Hypotheses such as these could be developed and tested for other phenological asynchronies. Here, we propose a framework for studying ecosystem responses to phenological mismatches: (i) focus the research on systems where long-term phenological data exist and, thus, changes over decades, perhaps even longer, can be modeled and investigated; (ii) identify species with a degree of seasonality influenced by climate change; (iii) investigate ecosystems where the interactions of the study species (ideally only a few) are primary drivers of ecosystem functioning. While any interaction may have a measurable effect on some ecosystem function, such a focus will ensure that the results are relevant and will address the difficulty of including additional study species (although this will be required in some systems); (iv) design experiments that manipulate the timing of at least two species in different trophic levels in ways that represent current and potential future conditions. Experimental studies may, by necessity, focus on short-term responses. If possible, the experiment should be conducted over multiple years with the phenological shifts in the same direction to determine the ecosystem response of interest in the longer term; (v) measure and model the ecosystem response of interest under both current conditions and future climate scenarios. Ecosystem measurements, such as CO_2 and trace gas exchanges, or forage nutrition, should not be any more difficult to measure in phenological mismatch studies than in any other study measuring ecosystem responses; and (vi) combine experimental and modeling approaches where possible to address the potential limitations of either method.

Concluding Remarks and Future Directions

Phenological mismatch studies should no longer ignore ecosystem responses. Long-term data sets showing phenological change, particularly of more than one trophic level, are key to designing and conducting future studies investigating these responses. Long-term phenology data are being extracted from herbarium specimens and collected by organizations, including the National Phenology Network (NPN) and National Ecological Observatory Network (NEON) in the USA, and globally by the International Long Term Ecological Research Network (ILTER) and eBird, but multitrophic level studies may require combining data sets in creative ways. It is critical that phenological data collection continues for decades to inform realistic experiments.

A recent study showed that changing phenology between overstory and understory vegetation in Thoreau's Woods in Massachusetts, USA, influenced C budgeting, and provides an example of how long-term data sets can be used to make these types of projections [12]. Here, we focus on how phenological mismatch influences ecosystem functioning, namely nutrient cycling, but future studies could focus on the effects to ecosystem services that more directly link to humans, such a food provisioning or flood regulation.

Acknowledgments

Work was funded by National Science Foundation (NSF) awards 1304523 and 1304879, by the Utah Agricultural Experiment Station, Utah State University, and South Dakota Agricultural Experiment Station, and approved as journal paper #9219. Data are published online at the NSF Arctic Data Center (doi: 10.18739/A22274). Figures were prepared with the help of Ryan Choi, who also took the brant photos included. Art in Figure 2 was provided by shutterstock.com and the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

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https://doi.org/10.1016/j.tree.2019.07.019

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