Creative citizen science illuminates complex ecological responses to climate change

Abraham J. Miller-Rushing^{a,1}, Amanda S. Gallinat^{b,c}, and Richard B. Primack^d

Climate change is causing the timing of key behaviors (i.e., phenology) to shift differently across trophic levels and among some interacting organisms (e.g., plants and pollinators, predators and prey), suggesting that interactions among species are being disrupted (1, 2). Studying the phenology of interactions, however, is difficult, which has limited researchers' ability to zero in on changes in specific interactions or on the consequences of mismatches. In PNAS, Hassall et al. (3) use a combination of citizen science techniques to investigate the effects of climate change on dozens of specific interactions. They focus on a Batesian mimicry complex involving stinging bees and wasps, stingless syrphid flies (also known as hoverflies) that mimic their appearance, and avian predators. The methods used by Hassall et al. (3) continue an upsurge of innovations in climate change ecology research, in which the role of citizen science is expanding to provide new approaches to complex challenges.

Citizen Science Has a Long History in Ecology and Climate Change

Citizen science (i.e., the participation of nonspecialists in scientific research) has yielded important contributions throughout the history of ecology (4). Our understanding of ecological and phenological responses to climate change, in particular, has benefited from long-term observations collected by individuals and networks, like those of naturalists Henry David Thoreau and Robert Marsham (5, 6) and historical phenology and weather observation networks (7), and the ongoing insect monitoring schemes used by Hassall et al. (3). It is this type of citizen science-enthusiastic volunteers collecting and submitting field observations-that many people imagine when they think of citizen science in ecology. In fact, the amount of data being generated from these types of observations is staggering; citizen scientists have recorded hundreds of millions of observations, yielding much of the existing data describing how flowering, bird migration, and

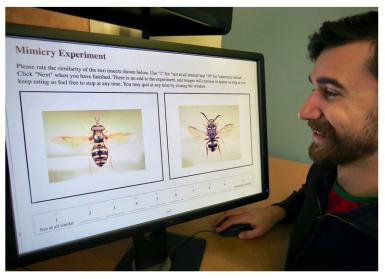


Fig. 1. The online game Hassall et al. (3) created to identify hymenopteran model (Right) and syrphid mimic (Left) pairs, in action.

insect flight times are changing (8-10). These observations, as many as there are, account for only a small portion of the growing breadth of projects and ways to engage citizen scientists (11). For example, citizen scientists are categorizing, describing, and transcribing digital images and museum specimens (12); community members are working jointly with researchers on all stages of some research projects (13); and volunteers are developing new technologies for open research (14).

Why Studying Interactions or Mismatches Is Hard

The methodology of Hassall et al. (3) gives us a way to approach notoriously difficult-to-study questions about species interactions and temporal mismatches. Ecologists have speculated that phenological mismatches may be occurring throughout nature, disrupting ecological relationships; however, this speculation has been accompanied by surprisingly little evidence

^aAcadia National Park, National Park Service, Bar Harbor, ME 04609; ^bDepartment of Biology, Utah State University, Logan, UT 84322; ^cEcology Center, Utah State University, Logan, UT 84322; and ^dDepartment of Biology, Boston University, Boston, MA 02215 Author contributions: A.J.M.-R., A.S.G., and R.B.P. wrote the paper.

See companion article 10.1073/pnas.1813367115.

The authors declare no conflict of interest

Published under the PNAS license.

¹To whom correspondence should be addressed. Email: abe_miller-rushing@nps.gov.

(15). Research is limited by the difficulty of examining interactions in the field and the possibility that mismatches may be uncommon or quickly corrected by evolutionary processes (15), and many interactions are hidden or would take too much time to observe. In cases of mimicry, like those studied by Hassall et al. (3), identifying model-mimic pairs can require complex measurements and comparisons of morphology. As a result, testing the influence of shifts in phenology on the fitness of organisms is rare (but see refs. 16 and 17). In the case of model species, mimics, and predators, measuring the fitness consequences of phenological change can require experiments to test predator preference or behavior, but such experiments are difficult to carry out and might have unexpected artifacts depending on their design.

New Approaches to Investigating Interactions

In recent decades, new technologies have paved the way for more indirect approaches—for example, environmental DNA, satellite tracking, and time-lapse videos or camera traps—to investigate interactions among species. These techniques enhance our ability to assess which species are in the same locations at the same times and to document occurrences of specific interactions that might get captured on camera. But they leave open questions about the nature of interactions and the consequences of phenological shifts on interacting species. The approach of Hassall et al. (3) shows one way to fill these gaps; their unusual methodology allowed them to investigate dozens of interactions across complex trophic relationships. Each step of their approach demonstrates a unique value of citizen science that other researchers might find useful in their own work.

First, rather than observing model-mimic relationships directly in the field or using feeding tests with birds, Hassall et al. (3) created an online game in which citizen scientists could rate the visual similarities of co-occurring pairs of syrphids and hymenopterans based on size, shape, color, hairiness, and other characters (Fig. 1). Over the course of a year, volunteers (recruited via Twitter) submitted 30,300 ratings and identified 237 high-fidelity modelmimic pairs out of 2,352 potential combinations, with results that correlated strongly with pigeon experiments. This technique demonstrates the value of citizen science to allow researchers to assess pairwise combinations faster and in greater numbers than can be achieved using traditional methods. Variations on this method could be appropriate for other studies involving morphological comparisons, such as in other model-mimic or camouflage studies, or studies of specimens collected during bioblitzes or biodiversity inventories.

Second, Hassall et al. (3) analyzed over a million records of syrphid fly, bee, and wasp abundance from two long-term citizen science monitoring projects in the United Kingdom. This extensive dataset showed that hymenoptera emerge earlier, on average, than syrphid flies, and that the spring emergence of hymenopterans is advancing faster than that of syrphids in response to warming temperatures. This study adds to the growing body of research using citizen science data to document shifts in species phenology and interactions, including community-level interactions at single locations (18), possible interactions across trophic levels (1), and known interactions (2).

Third, Hassall et al. (3) developed a virtual reality game to simulate model-mimic-predator interactions in different phenological scenarios. Instead of offering live hymenopterans and syrphids to birds in complicated feeding experiments, or using data-intensive and highly parameterized computational algorithms, 45 humans took on the role of bird predators in a game. Participants were recruited from the University of Leeds and surrounding areas and were compensated £5 for their time. They gained points by feeding on benign mimic syrphids and lost points when they ate stinging model hymenopterans. Participants had to identify mimics against complex backgrounds, a simulation of the challenges that bird predators face in deciding whether or not to feed on an insect. The results of the game showed that model species (i.e., bees and wasps) perform best (i.e., had highest survival rates) when they are active before the syrphid mimics. Mimics, on the other hand, perform best when the phenology of model species and mimics overlaps and occurs randomly from the perspective of predators.

In PNAS, Hassall et al. use a combination of citizen science techniques to investigate the effects of climate change on dozens of specific interactions.

And predators do best when either the model bees and wasps emerge first or when the syrphid mimics emerge first, with consistency. This creative game-based approach worked because researchers could be fairly confident that decisions made by humans in simulations were similar to those previously observed in animal-based experiments and results from algorithms and neural nets. This technique could be promising in other ecological systems in which human behavior and decision making provides an added value, such as in other predator-prey, competition, or mutualism interactions.

Fourth, in the final phase of their study, Hassall et al. (3) returned to the long-term citizen science data to analyze changes in the phenology of the interacting species as the climate warms in light of what they discovered about the fitness benefits and costs of different phenological scenarios. They found that the phenology of many model bee and wasp species is shifting so that they appear before mimic syrphid species. These shifts create new situations that benefit bees and wasps and bird predators, while reducing the circumstances during which syrphids do best (overlapping phenology) and worst (mimics emerge first). These conclusions result from the synthesis of three citizen science tools, each of which benefitted from different styles and values of participant contributions, and each of which provided a different piece of this complex story.

What Next?

The approaches of Hassall et al. (3) avoid labor-intensive field research and sometimes impossible-to-get direct observations of interactions in nature. We are confident that researchers will find many more applications for these techniques. Most obviously, similar methods might be applied to other Batesian mimicry systems such as those occurring in butterflies, in which there are models, mimics, and bird predators (e.g., 19). This approach might also be applied to other complex species interactions such as some predator-prey interactions, or to human activities such as bushmeat hunting or fishing strategies.

Moreover, the results of Hassall et al. (3) have intriguing implications and raise questions about their generality and how they play out in nature. Is selection driving these changes in phenology or are the hymenopteran model species just more phenotypically plastic than the mimic syrphids? The predictions generated from this study (and other such studies) should also be tested with field studies of the target species. Do syrphid mimics really do worse when they emerge before hymenopteran models? And do birds and hymenopterans do better when models emerge before mimics?

The approaches of Hassall et al. (3) add to the growing creativity of citizen science in ecology and climate change research. New technologies, the collection and sharing of large datasets, and greater online access to historical data and museum specimens contribute to this growth, as does the willingness and interest of so many people to participate in scientific projects. We hope that ecologists continue to apply new, innovative approaches to pressing current problems like understanding ecological responses to climate change.

Acknowledgments

We thank Rick Bonney, Christopher Hassall, Tom Sherratt, and Jake Weltzin for comments on earlier versions of this paper. The findings and conclusions in this paper are those of the authors and do not necessarily represent the views of the US Government.

- 1 Thackeray SJ, et al. (2016) Phenological sensitivity to climate across taxa and trophic levels. Nature 535:241–245.
- 2 Kharouba HM, et al. (2018) Global shifts in the phenological synchrony of species interactions over recent decades. Proc Natl Acad Sci USA 115:5211–5216.
- 3 Hassall C, Billington J, Sherratt TN (2019) Climate-induced phenological shifts in a Batesian mimicry complex. Proc Natl Acad Sci USA, 10.1073/pnas.1813367115.
- **4** Miller-Rushing A, Primack R, Bonney R (2012) The history of public participation in ecological research. *Front Ecol Environ* 10:285–290.
- **5** Sparks TH, Carey PD (1995) The responses of species to climate over two centuries: An analysis of the Marsham phenological record, 1736-1947. *J Ecol* 83:321–329.
- 6 Primack RB, Miller-Rushing AJ (2012) Uncovering, collecting, and analyzing records to investigate the ecological impacts of climate change: A template from Thoreau's Concord. *Bioscience* 62:170–181.
- 7 Schwartz MD, ed (2003) Phenology: An Integrative Environmental Science (Kluwer Academic Publishers, Dordrecht, The Netherlands), p 564.
- 8 Chandler M, et al. (2017) Contribution of citizen science towards international biodiversity monitoring. Biol Conserv 213:280–294.
- 9 Theobald EJ, et al. (2015) Global change and local solutions: tapping the unrealized potential of citizen science for biodiversity research. Biol Conserv 181:236–244.
- 10 Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37-42.
- 11 Shirk J, et al. (2012) Public participation in scientific research: A framework for deliberate design. Ecol Soc 17:29.
- 12 Ellwood ER, et al. (2015) Accelerating the digitization of biodiversity research specimens through online public participation. Bioscience 65:383–396.
- 13 Fernandez-Gimenez ME, Ballard HL, Sturtevant VE (2008) Adaptive management and social learning in collaborative and community-based monitoring: A study of five community-based forestry organizations in the western USA. *Ecol Soc* 13:4.
- 14 Austen K (2015) Environmental science: Pollution patrol. Nature 517:136-138.

15 Renner SS, Zohner CM (2018) Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. Annu Rev Ecol Evol Syst 49:165–182.

- 16 Zimova M, Mills LS, Nowak JJ (2016) High fitness costs of climate change-induced camouflage mismatch. Ecol Lett 19:299–307.
- 17 Reed TE, Jenouvrier S, Visser ME (2013) Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. J Anim Ecol 82:131–144.
- 18 Ovaskainen O, et al. (2013) Community-level phenological response to climate change. Proc Natl Acad Sci USA 110:13434–13439.
- 19 Ries L, Mullen SP (2008) A rare model limits the distribution of its more common mimic: Atwist on frequency-dependent Batesian mimicry. *Evolution* 62:1798–1803.