Citizen scientists document geographic patterns in pollinator communities

Alison J. Parker* and James D. Thomson

University of Toronto, Department of Ecology and Evolutionary Biology, 25 Harbord Street, Toronto, Ontario M5S 3G5 Canada

Abstract—It is widely recognized that plants are visited by a diverse community of pollinators that are highly variable in space and time, but biologists are often unable to investigate the pollinator climate across species' entire ranges. To study the community of pollinators visiting the spring ephemerals *Claytonia virginica* and *Claytonia caroliniana*, we assembled a team of citizen scientists to monitor pollinator visitation to plants throughout the species' ranges. Citizen scientists documented some interesting differences in pollinator communities; specifically, that western *C. virginica* and *C. caroliniana* populations are visited more often by the pollen specialist bee *Andrena erigeniae* and southern populations are visited more often by the bombyliid fly *Bombylius major*. Differences in pollinator communities throughout the plants' range will have implications for the ecology and evolution of a plant species, including that differences may affect the male fitness of individual plants or the reproductive success of plant populations, or both.

Keywords: citizen science, plant-pollinator interactions

Introduction

A rich history of research has explored the role of a pollinator species in determining the reproductive success of a plant, selecting for plant traits, and in some cases influencing reproductive isolation (van der Niet et al. 2014). We know that most plants are visited by a diverse community of pollinators (Waser et al. 1996), and that the diverse community of pollinators can be highly variable geographically (Herrera et al. 2006). Yet the vast majority of studies of plant-pollinator interactions are conducted in one geographic location; Herrera et al. (2006) calculates that 88.4% of plant-pollinator studies look at only one site.

The diversity and abundance of pollinators visiting a plant population in any given location and time form the "pollinator climate" (Grant & Grant 1965). A number of studies have documented variation in the pollinator climate in different plant populations within the same plant species. Most studies focus on a small number of sites (e.g. Miller 1981; Robertson & Wyatt 1990; Arroyo & Dafni 1995; Johnson & Steiner 1997; Price et al. 2005), and many are confined to a relatively small geographic area (e.g. Miller 1981; Robertson & Wyatt 1990; Arroyo & Dafni 1995; Johnson & Steiner 1997; Price et al. 2005; Gomez et al. 2008). These studies have contributed to the understanding that pollinator communities are variable. However, in the majority of studies there is no obvious pattern or process that explains the documented variation in pollinator communities, so the conclusions to these studies are limited to the specific populations studied.

Looking for and documenting large-scale patterns in pollinator communities requires a great deal of observational data. Studies are often limited to just one or a few plant populations (Herrera et al. 2006). Some limitations are specific to plant-pollinator studies; often the flowering season of a study species will limit the time available for traveling throughout the plant range, and pollinator identification can be very difficult for novice research assistants (Lye et al. 2011; Kremen et al. 2011). Recently, more and more biologists have begun to employ the efforts of amateur naturalists and volunteers in their research efforts (Dickinson et al. 2010; Silvertown 2009). Citizen scientists can benefit research in ecology and evolution in many ways, including expanding the scope of data collected over space and time, filling gaps in natural history knowledge, and increasing access to otherwise inaccessible spaces, such as private land (e.g., Lye et al. 2011 recruited volunteers to document bumblebee nest sites in their private gardens). Citizen science also provides an opportunity for scientists to connect with the public, hear valuable observations from residents of an area, and build public support for science and conservation (Dickinson et al. 2010; Cooper et al. 2007; Toomey & Domroese 2013; Lewandowski & Oberhauser 2017; McKinley et al. 2017; Ballard et al. 2017). In pollination research especially, there is great potential for harnessing the enthusiasm of amateur naturalists to support large-scale data collection and fill in gaps in our understanding of the basic natural history and biogeography of plants and pollinators. Citizen scientists are a great resource for pollinator monitoring; often, amateur naturalists have practice in plant and insect identification, are eager to spend time outdoors to contribute to monitoring, and are already located throughout the range of the plant and pollinator species of interest (Kremen et al. 2011). Citizen science for the biology and conservation of *Danaus plexippus* (monarch) butterflies is a model for demonstrating the

potential impact of citizen science (Ries & Oberhauser 2015) and pollination citizen science projects such as the Great Sunflower Project and Bumble Bee Watch have made strong contributions to research in pollination and pollinator biology (Acorn 2017, Lye et al. 2011, Birkin et al. 2015, Roy et al. 2016, Deguines et al. 2012). Except for these efforts, citizen science is relatively underused in pollination research and has potential to add greatly to our understanding of pollination and pollinator biology. Kremen et al. (2011) compared data sets of pollination observations collected by citizen scientists to data sets collected by experts, and found that although the citizen scientists missed some taxonomic diversity, the qualitative results were comparable. Citizen science data can help identify how the pollinator climate varies in space and time, and help document large-scale geographic patterns in a plant species' pollinator climate (Dickinson et al. 2010).

To better understand patterns in pollinator climates, we recruited citizen scientists to do pollinator observations across the range of two plant species, *Claytonia virginica* and *Claytonia caroliniana*. Specifically, we ask: 1) Do pollinator climates vary along large-scale patterns like latitude, longitude, and altitude? 2) By conducting observations over an entire species' range, can we uncover patterns in variation in pollinator diversity and abundance? Previous observations caused us to predict that the pollinator climate of *C. virginica* and *C. caroliniana* would vary latitudinally, with higher fly visitation in Southern populations (Parker et al. 2017).

Materials and methods

Claytonia virginica and *Claytonia caroliniana* (Portulacaceae), collectively known as "spring beauty", are spring ephemeral wildflowers native to North American eastern woodlands, where they are visited by a variety of insects, among them the oligolectic solitary bee *Andrena erigeniae*, which collects pollen exclusively from these two species (Fig. 1). Female bees may eat some pollen, but most pollen is used to provision *A. erigeniae* larvae. These two species of *Claytonia* and *A. erigeniae* have overlapping geographic ranges and are phenologically matched (Davis & LaBerge 1975). A number of generalist species also visit *C. virginica* and *C. caroliniana*, collecting pollen or nectar from these plants and other sources. The generalist bee species are from many genera and include both pollen-foragers and social parasites that do not amass pollen provisions. The other most frequent visitor, the bee fly *Bombylius major*, is focused on nectar-collecting and mostly ignores pollen. *Bombylius major* is a parasite of solitary bee species, probably including *Claytonia*'s oligolege *A. erigeniae*. The distribution of these *Claytonia* species ranges from Georgia to Ontario, and from the East Coast west to Kansas and Nebraska. These species are protandrous; pollen and nectar are offered on the first day, in the male phase, while only nectar is produced in the succeeding female phase (Fig. 1).

To recruit volunteers, we advertised the project on established email listservs, including Native Plant Societies and Master Gardener lists. Hundreds of volunteers responded with interest and ultimately, 27 people submitted usable data. The instructions and learning materials for participating in the project were compiled onto a website. Before participating, we asked volunteers to visit the website, familiarize themselves with the project protocol, and study the identification of the bees and flies that they were likely to see in the field. Volunteers were also responsible for locating a patch of *C. virginica* or *C. caroliniana* in their local area; these patches could be in any habitat type. Volunteers were able to ask questions via email and also on the project website, where they could view our responses to questions as well as respond to one another.

Volunteers throughout the range of the plants located a patch of *C. virginica* or *C. caroliniana* in their area, recorded general information about the site and patch, and conducted observations a few times throughout March, April and May of 2011, 2012, and 2013. We asked volunteers to conduct observations three times throughout the season, but many volunteers were only able to do two, and some conducted many more than three. Each set of observation periods included six five-minute observation periods, each focusing on a defined number of focal flowers. During observations, volunteers recorded the identity of visiting insects and the number of visits that each insect made to male- and female-phase flowers. To facilitate identification, we organized the floral visitors into groups according to taxon, morphology, and behaviour. We provided volunteers with an information sheet with photographs and distinguishing characteristics of these pollinator groups, including size, colour, and body shape; we asked that they refer to this sheet during observations (Fig. 2). We encouraged volunteers to use these groups but also allowed identifications at any level or descriptions of the visitor (e.g., "unknown", "unknown bee", "small black bee with yellow stripes"). After conducting observations, volunteers submitted their data by mailing in their original data sheets, by entering and emailing data on a spreadsheet that we provided, or by entering and emailing data on a fillable PDF of the data sheets. Following submission of data by volunteers, we reviewed the data submitted and removed submissions that did not follow the data collection protocol.

We encouraged volunteers to conduct observations on three different days throughout the season, and as much as possible on sunny days between 10 am and 12:30 pm. On each day of observations, volunteers recorded information on the date, site, and plants, including the location, the plant species observed, and the phenology of the plant individuals. Before each set of observation periods, volunteers recorded the temperature and provided a general rating of the amount of wind and cloud cover. Before each observation period, volunteers defined an observation area that included a number of flowers; volunteers chose the number of flowers that they observed during each observation period. Volunteers observed different flowers in each observation period, though in small patches the flowers may have been very close to one another. They defined their area of observation by using a hula hoop or other square or circular perimeter. Volunteers identified how many of their focal flowers were male-phase and how many were female-phase, using an information sheet that contained detailed photographs and outlined the morphological differences between male- and female-phase flowers. Before beginning their observation period, volunteers set a stopwatch for five minutes.

Figure 1.   Photos of the *Claytonia virginica* pollination system. (A) A *C. virginica* female-phase flower. (B) A *C. virginica* male-phase flower. (C) The bee-fly *Bombylius major* visiting *C. virginica*. (D) The oligolectic bee *Andrena erigeniae* visiting *C. virginica*. (Reprinted from Parker et al. 2016)

During each five-minute observation period, volunteers observed their focal flowers. When an insect visited, volunteers recorded the identity of that visitor to the best of their ability and recorded the number of male- and female-phase visits that visitor made. Volunteers counted the number of total visits regardless of whether they were made by the same pollinator individual or different individuals. When identifying insects, we encouraged volunteers to use the functional groups that we provided; however, if the volunteer was not sure of the identification, the volunteer identified the insect as "unknown".

All statistical analyses were done using generalized linear mixed models (GLMMs) in *R 3.0.1* (R Core Team 2013). The function *glmmADMB* in the R library *glmmABMB* (Fournier et al. 2012) allowed us to account for highly variable observation times, include random effects, and account for overdispersion in the response variables. We analysed the total number of visits from a visitor group in thirty minutes, including re-visits. The response variable was the number of visits by any individual in a particular floral visitor group in 30 minutes; groups of floral visitors included *A. erigeniae, B. major*, small dark bees, parasitic bees, other bees, other flies, all bees, and all flies. At the start, we included the following predictor variables in each model: latitude; longitude; the interaction between latitude and longitude; elevation; whether observations were conducted in a designated natural area/park or a residential area; in natural areas, the approximate size of the park where observations

were conducted; the plant species observed (*C. virginica* or *C. caroliniana*); the temperature; the approximate level of wind (windy, light breeze, or still); the approximate degree of cloud cover (sunny, partly cloudy, or overcast); and the proportion of flowers observed that were male-phase flowers. When one of these factors did not improve the model fit, as indicated by log likelihood ratios, we removed it from the final model. Of these response variables, all final models included only latitude, longitude, and whether observations were conducted in a designated natural area/park or a residential area, because the remaining response variables did not improve model fit. To account for the high variation in the number of flowers observed and number of observation periods conducted, we included the total number of flowers observed as an offset. Because visits observed by a volunteer on a particular day are not independent, we included this as a random effect; as such, each day of observations for a particular volunteer represents the level of replication in each model. To account for overdispersed data, we used a negative binomial error distribution. Because weather influences pollinator visitation, we also ran each of the models with significant results on a subset of the data that included only those observations that occurred when the temperature was above 15°C. These models produced qualitatively similar results to those presented here.

Results

We received usable data from 27 volunteers over three years, who together conducted 655 observation periods (95
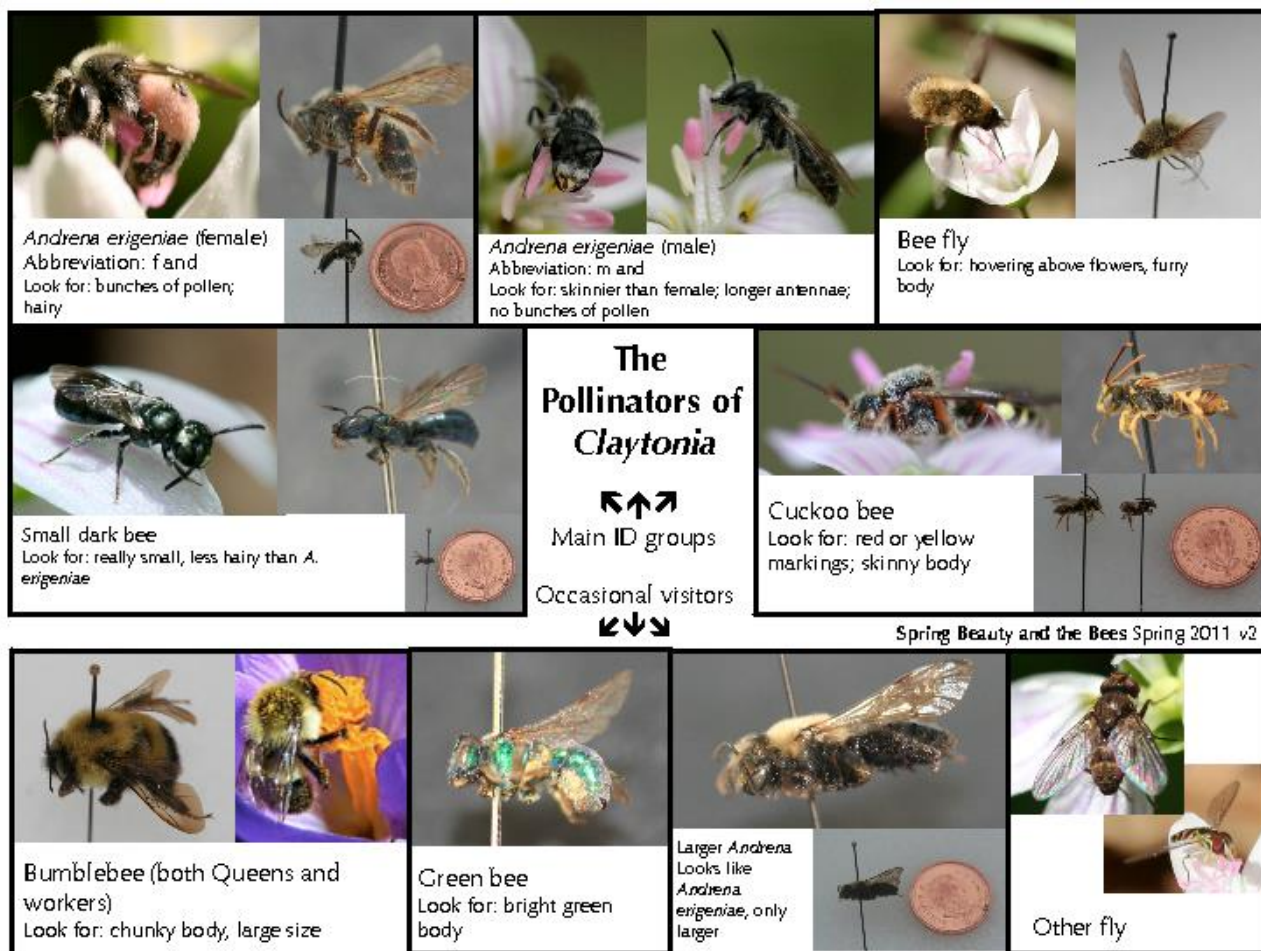
FIGURE 2. Volunteer information sheet with photographs and distinguishing characteristics of these pollinator groups, including size, colour, and body shape; we asked that they refer to this sheet during observations

sets of six five-minute observation periods) and observed a total of 14,159 flowers (Fig. 3). Observations were submitted from 24 locations ranging from Vermont to Wisconsin to Kansas, with high representation from Maryland and Virginia. Within these data (1,328 insect visits), 46.46% of insect visits were reported as *A. erigeniae*, 10.24% as *Bombylius major*, 23.87% small dark bees, 3.6% parasitic bees, 3.92% other bees, 9.49 other flies, and 2.41% unspecified. All categories of visitors were included in analyses (as follows), with the exception of unspecified insects, or entries marked as "unknown"; these were excluded.

The number of visits by the pollen specialist bee *A. erigeniae* in 30 minutes (one set of observation periods) varied significantly with longitude, with more visits in the western part of the range than the eastern (Tab. I, Fig. 3C, $Z = 2.62$, $P = 0.0088$). The number of visits by the bombyliid fly *B. major* in 30 minutes varied significantly with latitude, with more visits in the southern part of the range than the northern (Tab. I, Fig. 3B, $Z = 3.25$, $P = 0.0011$). There was no significant effect of latitude on *A. erigeniae* visitation (Tab. I, Fig. 3D, $Z = 0.40$, $P = 0.687$, and no significant effect of longitude on *B. major* visitation (Tab. I, Fig. 3A, $Z = 0.29$, $P = 0.772$). The type of land use in the local area of the observations (whether the observations were done in a residential area or in a natural area) had a significant effect on

the model fit, with higher *A. erigeniae* visitation in natural areas than residential areas.

The number of visits by small dark bees, parasitic bees, other bees, other flies, all bees, and all flies did not vary significantly with latitude or longitude, and for the most part none of the other predictor variables included in the model had a significant effect on visitation by these insects. The exception is that there were more visits by other flies when there was a higher proportion of male-phase flowers observed ($Z = 2.67$, $P = 0.0076$).

DISCUSSION

Data collected by citizen scientists revealed a significant effect of large-scale geographic parameters on the number of visits by two important pollinators of *C. virginica* and *C. caroliniana* in thirty minutes. In other words, the pollinator climate – i.e., the diversity and abundance of *A. erigeniae* and *B. major* specifically – changes fairly predictably along both a latitudinal gradient and a longitudinal one. In lower latitudes, *Claytonia* populations are visited by more bombyliid flies; in western populations, *Claytonia* populations are visited by more *A. erigeniae* bees. These patterns are consistent with the high visitation rates of *B. major* to *C. virginica* documented by Motten et al. (1981) in North Carolina, as well as with our
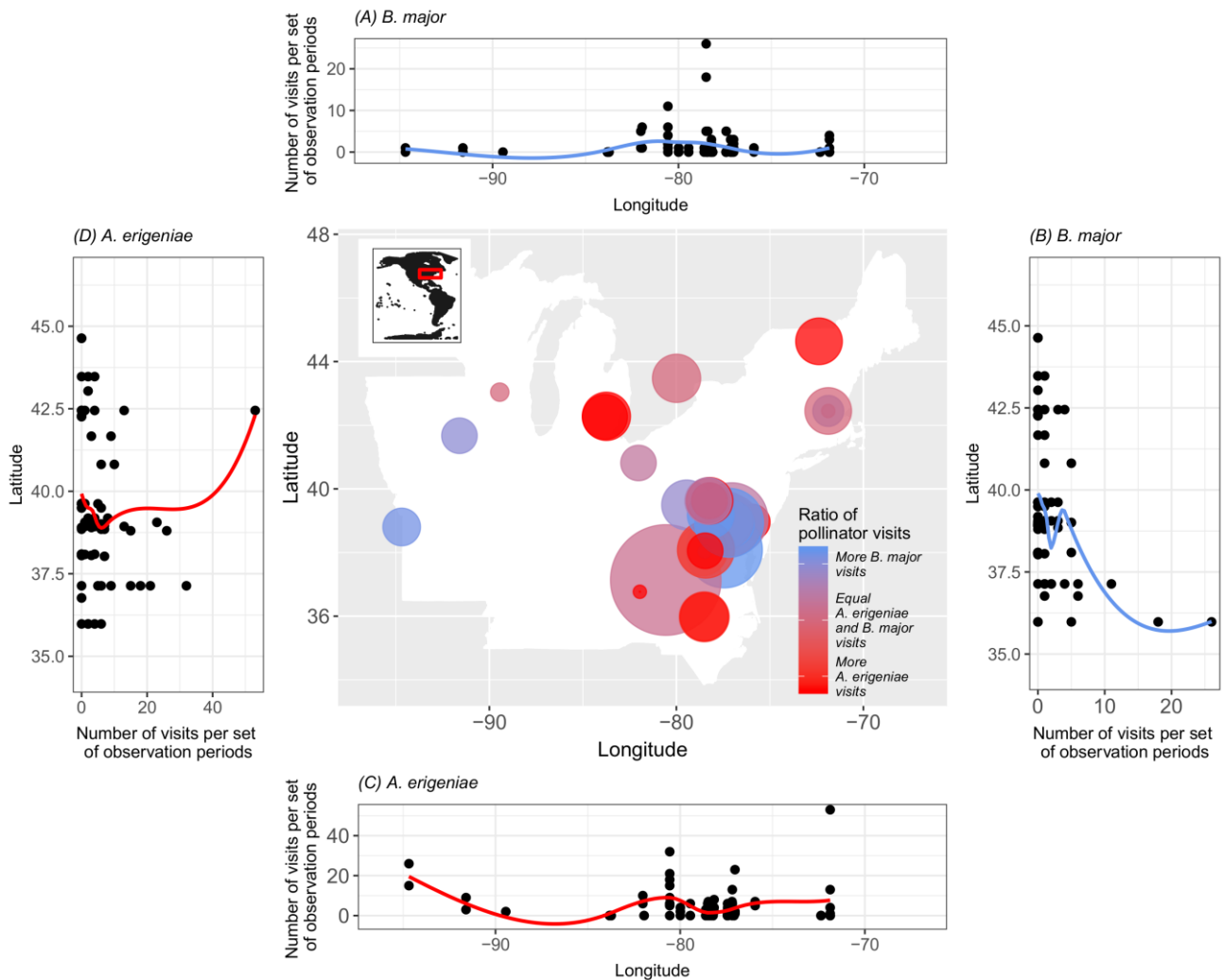
FIGURE 3.   Patterns in *A. erigeniae* and *B. major* visitation to *C. virginica* and *C. caroliniana*. (A) The relationship between longitude and the number of visits by *B. major* per set of observation periods. Curves were fit using locally weighted least squares (LOWESS). (B) The relationship between latitude and the number of visits by *B. major* per set of observation periods. Curves were fit using locally weighted least squares (LOWESS). (C) The relationship between longitude and the number of visits by *A. erigeniae* per set of observation periods. Curves were fit using locally weighted least squares (LOWESS). (D) The relationship between latitude and the number of visits by *B. major* per set of observation periods. Curves were fit using locally weighted least squares (LOWESS). (E) Ratio of pollinator visits at each site of pollinator observations. Ratios are calculated as the number of *A. erigeniae* visits over the number of *A. erigeniae* and *B. major* visits. The colour represents the ratio of pollinator visits, with more blue circles representing higher ratios of *A. erigeniae* visits, and more red circles representing lower ratios of *A. erigeniae* visits, which corresponds with higher ratios of *B. major* visits. The size of the circles represents the number of sets of observation periods conducted at each site. Axes in (A), (B), (C), and (D) correspond with the direction of latitude and longitude in (E).

own observations of visitation rates in Pennsylvania, Maryland, and North Carolina (Parker et al. 2017). We cannot explain the more specific factors that may be impacting these patterns. They may result from variation in the abundance of insect populations. Despite its importance, we do not understand the factors that underlie bee and fly population dynamics very well (Bischoff 2003; Franzen & Nilsson 2013) and we may under-estimate the value of flies as pollinators (Kearns 2001). The results of this study may be driven by biology; for example, flies are more common in cool, moist habitat and have lower energy requirements (Kearns 2001). Another driving factor may be the relationship of these species to one another. *Bombylius major* is a parasite of solitary bees, including *Andrena*, and therefore may be

parasitizing *A. erigeniae* populations. It is hard to say how this relationship impacts the differences observed here, as one would expect that their abundances would be correlated, but we are not aware of *B. major* visiting other plants in northern regions and *A. erigeniae* does not appear to visit plants besides *C. virginica* when *B. major* is abundant (pers. obs.)

Instead, the patterns in our data may result from changes in relative numbers of visits due to variation in floral attractiveness, the composition of plant communities, or some other factor. In general, our results indicate that large-scale geographic gradients – those patterns that change with latitude and longitude – are likely to be important. Climate, day length, and the range limits of interacting species are some

TABLE 1. Results of generalized linear mixed models. The response variable is the number of visits by any individual in a particular floral visitor group in 30 minutes ($N = 95$). *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Andrena erigeniae	Estimate	Standard	Z value	P value
Latitude	0.0387	0.0960	0.40	0.687
Longitude	-0.1048	0.04	2.62	0.0088**
Residential or Natural Area	-1.529	0.449	3.40	0.00066***
Bombylius major				
Latitude	-0.3310	0.1018	3.25	0.0011**
Longitude	0.0158	0.0544	0.29	0.7715
Residential or Natural Area	0.0643	0.4415	0.15	0.8842

intriguing possibilities that deserve attention in future research.

Because we documented gradients in the number of visits by two significant pollinators of *Claytonia*, we have a better idea of the pollinator climate experienced by plant populations in different parts of the species' range; western populations are visited more often by the oligolege *A. erigeniae*, while southern populations see *B. major* more often. We can now make predictions about how plant populations may respond these differences. The pollinators *A. erigeniae* and *B. major* are very different; the pollen specialist *A. erigeniae* is an adept and systematic forager that collects a great deal of pollen, while the bombyliid fly *B. major* is a haphazard forager that collects and deposits pollen only passively (Motten et al. 1981). Although the two pollinators deliver similar numbers of grains, *A. erigeniae* removes substantially more pollen during visitation than *B. major* (Parker et al. 2016). These results help identify traits that vary geographically that otherwise would be overlooked; in fact, Parker et al. (2017) describe ecotypic variation in pollen-related plant traits in *C. virginica* that corresponds with the pollinator climate.

Our approach was to recruit as many volunteers as possible, train volunteers remotely to the best of our ability using visual guides and specific protocols, gather as many data as possible, and identify and remove those data that did not follow protocol. We targeted recruitment efforts to organizations already familiar with plant and insect species identification (e.g. master naturalists) and targeted the more rural areas of the plant species' geographic range to promote geographic coverage. Beyond those initial efforts, we did not attempt to control participants' qualifications or balance geographic coverage in the resulting dataset. The purpose of this project was to provide a sense of the pollinator climate over a larger spatial and temporal scale and generate hypotheses about spatial and temporal patterns for future study. We supplemented these observations by examining patterns in the pollinator climate and pollen-related plant traits in more detail in specific locations (Parker et al. 2017). In this way, the value of these data collected are "fit for purpose"; other citizen science projects designed for other purposes may employ additional data validation methods, such as the validation of identification through photographs (Kremen et al. 2011, Wiggins et al. 2011, Lye et al. 2011), or

employ strategies for increasing or balancing geographic coverage and potential bias.

The use of citizen science provided a landscape-level view of variation in the pollinator climate, which otherwise would not have been possible. Aspects of this project made it especially conducive to citizen scientist participation. The two pollinators of greatest interest in this study (*A. erigeniae* and *B. major*) are very different morphologically and behaviourally and are relatively easy to distinguish from one another. *Claytonia* is abundant in many areas across its geographic range, and many participants already had a connection to local *Claytonia* populations from local parks or even their own property. Although some volunteers sent in images with their observations, we did not specifically test the accuracy of citizen scientists' differentiation among the pollinator groups; instead, we relied on the citizen scientists to follow protocols for species identification or indicate that they were unable to do so (e.g. by recording visitors as "unknown"). We reviewed the data submitted and removed those data that were not collected using the project protocol. This type of "expert review" is employed by 77% of citizen science projects, often accompanied by other data validation methods (Wiggins et al. 2011).

Citizen science is a novel approach for contributing to the foundation of knowledge in the biogeography of pollination systems. Without citizen science, we could not have obtained these data – or this coverage of *Claytonia*'s range – during *Claytonia*'s limited flowering period. Future studies that employ citizen science methods for studies of plants and pollinators will further demonstrate the value of citizen science for a variety of uses in pollination biology. Perhaps most importantly, future work should study the value of citizen science for broader outcomes in pollination biology, including providing an opportunity for pollination biologists to connect with the public and enhancing public support for pollination biology and pollinator conservation (e.g. Lewandowski & Oberhauser 2017), just as the value of citizen science continues to be demonstrated for science generally (Stepenuck & Green 2015, Newman et al. 2017; McKinley et al. 2017; Ballard et al. 2017; Toomey & Domroese 2013).

ACKNOWLEDGEMENTS

REFERENCES

Armbruster WS (1985) Patterns of character divergence and the evolution of reproductive ecotypes of *Dalechampia scandens* (Euphorbiaceae). Evolution 39:733-752.

Arroyo J, Dafni A (1995) Variations in habitat, season, flower traits and pollinators in dimorphic *Narcissus tazetta* L. (Amaryllidaceae) in Israel. New Phytologist 129:135–145.

Ballard HL, Robinson LD, Young AN, Pauly GB, Higgins LM, Johnson RF, Tweddle JC (2017) Contributions to conservation outcomes by natural history museum-led citizen science: Examining evidence and next steps. Biological Conservation 208: 87-97.

Birkin L, Goulson D (2015) Using citizen science to monitor pollination services. Ecological Entomology (2015) 40: 3-11.

Bischoff I (2003) Population dynamics of the solitary digger bee *Andrena vaga* Panzer (Hymenoptera, Andrenidae) studied using mark-recapture and nest counts. Population Ecology 45:197–204.

Boyd A (2002) Morphological analysis of Sky Island populations of *Macromeria viridiflora* (Boraginaceae). Systematic Botany 27:116–126.

Boyd AE (2004) Breeding system of *Macromeria viridiflora* (Boraginaceae) and geographic variation in pollinator assemblages. American Journal of Botany 91:1809–1813.

Cane JH, Sipes S (2006) Floral specialization by bees: analytical methodologies and a revised lexicon for oligolecty. In: Waser N, Ollerton J (eds.) Plant-Pollinator Interactions: From Specialization to Generalization. University of Chicago Press.

Cooper CB, Dickinson J, Phillips T, Bonney R (2007) Citizen science as a tool for conservation in residential ecosystems. Ecology and Society 12:11.

Darwin C (1877) On the various contrivances by which British and foreign orchids are fertilised by insects. J. Murray.

Davis LR, LaBerge WE (1975) The nest biology of the bee *Andrena (Ptilandrena) erigeniae* Robertson (Hymenoptera: Andrenidae). Illinois Natural History Survey Biological Notes 95: 1–24.

Deguines N, Julliard R, de Flores M, Fontaine C (2012) The whereabouts of flower visitors: Contrasting land-use preferences revealed by a country-wide survey based on citizen science. PLOS One 7(9):e45822.

Dickinson JL, Zuckerberg B, Bonter DN (2010) Citizen science as an ecological research tool: challenges and benefits. Annual Review of Ecology, Evolution, and Systematics 41:149-172.

Fournier DA, Skaug HJ, Ancheta J, Ianelli J, Magnusson A, Maunder MN, Nielsen A, Sibert J (2012) AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods Software 27:233–249.

Franzen M, Nilsson SG (2013) High population variability and source–sink dynamics in a solitary bee species. Ecology 94:1400–1408.

Galen C (1996) Rates of floral evolution: adaptation to bumblebee pollination in an alpine wildflower, *Polemonium viscosum*. Evolution 50:120-125.

Gomez JM, Bosch J, Perfectti F, Fernandez JD, Abdelaziz M, Camacho JPM (2008) Spatial variation in selection on corolla shape in a generalist plant is promoted by the preference patterns of its local pollinators. Proceedings of the Royal Society B 275:2241–2249.

Grant V, Grant KA (1965) Flower pollination in the phlox family. Columbia University Press.

Harder LD, Thomson JD (1989) Evolutionary options for maximizing pollen dispersal of animal-pollinated plants. American Naturalist 133:323–344.

Herrera CM (1995) Microclimate and individual variation in pollinators: flowering plants are more than their flowers. Ecology 76:1516-1524.

Herrera CM, Castellanos MC, Medrano M (2006) Geographical context of floral evolution: towards an improved research programme in floral diversification. In: Harder LD and Barrett SCH (eds), Ecology and evolution of flowers, Oxford University Press.

Hillebrand H (2004) On the generality of the latitudinal diversity gradient. American Naturalist 163:192–211.

Inoue K, Maki M, Masuda M (1996) Evolution of *Campanula* flowers in relation to insect pollinators on islands. In: Lloyd D and Barrett SCH (eds.) Floral Biology. Springer US, Boston, MA, pp 377-400.

Johnson SD (1997) Pollination ecotypes of *Satyrium hallackii* (Orchidaceae) in South Africa. Botanical Journal of the Linnean Society 123:225–235.

Johnson SD, Steiner KE (1997) Long-tongued fly pollination and evolution of floral spur length in the *Disa draconis* complex (Orchidaceae). Evolution 51:45-53.

Kearns C (2001) North American dipteran pollinators: assessing their value and conservation status. Ecology and Society 5(1):5.

Kremen C, Ullman KS, Thorp RW (2011) Evaluating the quality of citizen-scientist data on pollinator communities. Conservation Biology 25:607–617.

Lewandowski EJ and Oberhauser KS (2017) Butterfly citizen scientists in the United States increase their engagement in conservation. Biological Conservation 208: 106-112.

Lye GC, Osborne JL, Park KJ, Goulson D (2012) Using citizen science to monitor *Bombus* populations in the UK: nesting ecology and relative abundance in the urban environment. Journal of Insect Conservation 16:697-707.

MacArthur R (1984) Geographical Ecology. Princeton University Press.

Malo JE, Baonza J (2002) Are there predictable clines in plant–pollinator interactions along altitudinal gradients? The example of *Cytisus scoparius* (L.) Link in the Sierra de Guadarrama (Central Spain). Diversity and Distributions 8:365–371.

McKinley DC, Miller-Rushing A, Ballard HL, Bonney R, Brown H, Cook-Patton SC, Evans DM, French RA, Parrish JK, Phillips TB, Ryan SF, Shanley LA, Shirk JL, Stepenuck KF, Weltzin JF, Wiggins A, Boyle OD, Briggs RD, Soukup MA (2017) Citizen science can improve conservation science, natural resource management, and environmental protection. Biological Conservation 208: 15-28.

Miller RB (1981) Hawkmoths and the geographic patterns of floral variation in *Aquilegia caerulea*. Evolution 35:763-774.

Motten A, Campbell D, Alexander D, and Miller H (1981) Pollination effectiveness of specialist and generalist visitors to a North Carolina population of *Claytonia virginica*. Ecology 62:1278–1287.

Newman E, Manning J, Anderson B (2014) Matching floral and pollinator traits through guild convergence and pollinator ecotype formation. Annals of Botany 113:373-384.

Newman G, Chandler M, Clyde M, McGreavy B, Haklay M, Ballard H, Gray S, Scarpino R, Hauptfeld R, Mellor D, Gallo J (2017) Leveraging the power of place in citizen science for effective conservation decision making. Biological Conservation 208:55-64.

Parker AJ, Williams NM, Thomson JD (2016) Specialist pollinators deplete pollen in the spring ephemeral wildflower *Claytonia virginica*. Ecology and Evolution. doi:10.1002/ece3.2252

Parker AJ, Williams NM, Thomson JD (2017) Geographic patterns and pollination ecotypes in Claytonia virginica. Evolution doi:10.1111/evo.13381

Pérez-Barrales R, Arroyo J Armbruster WS (2007) Differences in pollinator faunas may generate geographic differences in floral morphology and integration in *Narcissus papyraceus* (Amaryllidaceae). Oikos 116: 1904-1918.

Price MV, Waser NM, Irwin RE, Campbell DR, Brody AK (2005) Temporal and spatial variation in pollination of a montane herb: A seven-year study. Ecology 86:2106–2116.

R Core Team (2013) R: A language and environment for statistical computing. Vienna, Austria.

Richards S, Williams N, Harder L (2009) Variation in pollination: causes and consequences for plant reproduction. American Naturalist 174:382–398.

Ries L, Oberhauser K (2015) A citizen army for science: Quantifying the contributions of citizen scientists to our understanding of monarch butterfly biology. BioScience 65: 419-430.

Robertson JL, Wyatt R (1990) Evidence for pollination ecotypes in the yellow-fringed orchid, *Platanthera ciliaris*. Evolution 44:121-133.

Roy HE, Baxter E, Saunders A, Pocock MJO (2016) Focal plant observations as a standardised method for pollinator monitoring: Opportunities and limitations for mass participation citizen science. PLOS One 11(3):e0150794.

Stepenuck KF, Green LT (2015) Individual- and community-level impacts of volunteer environmental monitoring: a synthesis of peer-reviewed literature. Ecology and Society 20(3): 19.

Toomey AH, Domroese, MC (2013) Can citizen science lead to positive conservation attitudes and behaviors? Human Ecology Review 20(1): 50-62.

van der Niet T, Peakall R, Johnson SD (2014) Pollinator-driven ecological speciation in plants: new evidence and future perspectives. Annals of Botany 113:199–211.

van der Niet T, Pirie MD, Shuttleworth A, Johnson SD, Midgley JJ (2014) Do pollinator distributions underlie the evolution of pollination ecotypes in the Cape shrub *Erica plukenetii*? Annals of Botany 113:301-315.

Williams NM, Winfree R (2013) Local habitat characteristics but not landscape urbanization drive pollinator visitation and native plant pollination in forest remnants. Biological Conservation 160:10–18.

Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. Annual Review of Ecology, Evolution, and Systematics 34:273–309.

Willmer PG (1983) Thermal constraints on activity patterns in nectar-feeding insects. Ecological Entomology 8:455–469.

Wiggins A, Newman G, Stevenson R, Crowston K (2011) Mechanisms for data quality and validation in citizen science. Proceedings of the 2011 IEEE Seventh International Conference on e-Science Workshops 14-19.

Winfree R, Bartomeus I, Cariveau DP (2011) Native pollinators in anthropogenic habitats. Annual Review of Ecology, Evolution, and Systematics 42:1–22.