DISSERTATION

WHERE HAVE ALL THE POLLINATORS GONE? AN ANALYSIS OF THE SHIFTS IN

CLIMATE AND PHENOLOGY THAT HAVE ALTERED POLLINATOR DIVERSITY IN

THE GREATER YELLOWSTONE ECOSYSTEM

Submitted by

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Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Spring 2023

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ABSTRACT

WHERE HAVE ALL THE POLLINATORS GONE? AN ANALYSIS OF THE SHIFTS IN

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Pollinators are in peril, facing worldwide decline due to causes such as climate change, habitat fragmentation, phenological mismatches, urbanization, pesticide use, agricultural intensification, and more. In the age of these challenges, prioritizing suitable habitat for species conservation is essential. United States (US) National Parks, in addition to other protected areas nationally and worldwide, act as species refuges for all biodiversity, including pollinators, and more specifically, butterfly and bumble bee species. While data availability is minimal to answer broad questions of pollinator decline, virtual datasets, including citizen science platforms and digitized Natural History Collections (NHCs), provide robust species occurrence snapshots to the state of biodiversity in the parks. This dissertation assessed pollinators, plant-pollinator relationships, and species responses to climate change in Yellowstone and Grand Teton National Parks, two parks within the Rocky Mountain region of the US. In the first chapter, I provide a literature review and my research framework that guided the following studies. In the second chapter, I conducted a meta-analysis to determine what species responses were worldwide to climate change effects. An analysis of the limited bumble bee literature showed species range contractions as well as detrimental plant-phenological shifts occurring worldwide. Although there were more butterfly studies, there was the most agreement found in earlier species emergence patterns, range contractions, and species generalist population responses. In the third

chapter, I analyzed digitized data within NHCs, citizen science platforms, and permit-reported data available for the parks from 1900-2021 to understand the systematic data gaps and taxonomic biases present within available datasets. I observed taxonomic biases and varying prominence within data repositories in both parks. However, the rate of available digitized records will continue to evolve and may shift these systematic gaps. In the fourth chapter, I evaluated the climate, phenology, and pollinator species occurrence relationships seen within the parks. I found that starting floral bloom dates and recent bloom anomalies have not shifted significantly, with an average earlier bloom date of three days observed across the parks. The correlations between phenological stages highlighted the negative effect of half-bloomed floral resources on pollinator occurrences in the subalpine and meadow areas of the park, and the positive effect of senesced floral resources on pollinator occurrences both habitat and park wide. Finally, the fifth chapter summarized with lessons learned, including species case studies, and suggestions for additional research efforts. These findings highlight the importance of continued monitoring of pollinator groups within the parks, particularly amongst groups with specialized plant-pollinator relationships, range restrictions, and sensitive generational production – all in which may be vulnerable in the age of a warming, drying western climate. Researchers can use these findings to inform land management and species conservation strategies, to prioritize useable and robust datasets of varying digitized availability for biodiversity questions, and to understand the baseline of pollinator data observed within two protected areas that have experienced minimized effects of other land-use pressures.

ACKNOWLEDGMENTS

My dissertation would not have been possible without the countless Pollinator Hotshots and graduate students who have chased butterflies down mountain sides and bees across flower-filled meadows. These field crews kept this project afloat, even amidst wildfires or summer snow, circumstances like vehicle breakdowns, bears on a trail, or other fieldwork woes, and even with the unprecedented COVID-19 pandemic. My deepest gratitude goes out to each of these

team members, whose future successes are just as important to me as this work. Through it all, I am leaving with not only a strong academic network but also friends who have become family that I am forever grateful to have met. The teams' diversity made this research effort even stronger as it opened my eyes up to different perspectives and helped me learn how to mentor and teach research skills. My gratitude goes out to the Colorado-Wyoming Louis Stokes Alliance for Minority Participation (CO-WY LSAMP), the Rocky Mountain Sustainability and Science Network (RMSSN), the University of Dijon (France), and the University of Derby (United Kingdom) for their student funding and recruitment that brought these teams together. 2017: Kenneth Choi, Autumn Harry, Nicole Wagner, Anne Le Mat, Nathan Tolle, Julia Tofan, Valentina Alvarez, Mahin Jalakhan, Isheka Orr, Mendrake "Obi" Sayee, and Benny Bonet. 2018: Ryan Gomez, Jordanne Pelkey, and Benjamin Duffy. 2019: Daniel Dominguez, Angelina Rivera, Esther Bourdon, and Luis Borrego. 2020: Cristal Dominguez Vasquez, Daniel Dominguez, Andrew Rohlf, Stella Stuchart, Nico Lucena, Cassidy Storey, Victoria Simon, and Soleil Culley. 2021: Daniel Lansidel, Katiana Garcia Rosado, Jacob Genuise, Alia Smith, and Whitney Valencia. 2022: Melissa Morales, Cristal Dominguez-Vasquez, Nicki Bailey, Alyssa Connaughton, Ashlee Hardin, Daniel Briggs, Kaiya Gibson, Tín Rodriguez, Mohammad Al-Mousa, Julien Paradis, Chloe Recouvreur, Madeline Gillet, and students from the University of Derby. Our bonds formed through these efforts extend beyond the internships or degrees we completed.

To my committee that helped me through this effort: thank you for all your resources, emails answered, space and time borrowed, and so much more. I stayed at Colorado State to pursue my PhD not only because of my love for this project and my research sites but also because of the people who supported me along the way. This dissertation would not have been

possible without all of you making me the scientist I am. To Meena, Emily, Arathi, and Paul: thank you for sharing your knowledge, for making me grow as a researcher, and for always being willing to provide feedback. I specifically want to thank Meena and Arathi for checking on me when work felt overwhelming and providing your own research and academic perspectives to learn from. Additionally, Meena and Emily helped me more than they realize, in both their assistance at the defense and in their dissertation suggestions, to finish this marathon of an effort. The committee dynamics evolved over my last year due to exciting opportunities and heartbreaking news, and I appreciate all that helped me persevere regardless of the circumstances.

I give a special thanks to Phil and Gillian for their mentoring throughout my research. To Phil: it is crazy that we ran into each other by circumstance on BioBlitz research back in 2016, and to see both of our careers evolve over time, in some instances together, has been so rewarding. Thank you for being a great mentor, colleague, and person who wants the best for all his students. I hope you can continue to mentor students and excel in the academic space, as your research and teaching interests are contributing to the educational greater good. To Gillian: I hope you can see my gratitude for you and all your research efforts. You have traveled thousands of miles with me, caught and photographed hundreds of insects for my dissertation, seen me laugh, cry, and lead teams, cooked and eaten many good meals but also some more questionable ones, and seen me grow as a person and scientist. We have had ups and downs in our work but have only come out stronger through those opportunities together. I hope my path continues to cross with all these amazing researchers I have looked up to during my time at Colorado State.

I want to remember and thank Paul Opler for his countless hours with me in the museum, providing his taxonomic expertise, and for helping me develop the primary butterfly guide for

advice, listen to my rants, and send me support when I didn't even know I needed it, thank you for being the greatest parents anyone could get. To my Uncle Art, who reinvigorated my passion and perseverance during my imposter syndrome days, I appreciate you reminding me of the joy behind our scientific work. To my grandparents, George, Martha "Toots", Morfar/Henry, and Mormor/Ullabritt, I thank you for supporting me through my academics so I could get to this stage in my career. I am so blessed to have the family that I do; they are nothing but supportive. The intelligence of all that raised me made me the person that I am today: book-smart, but also full of humility and grit. These skills cannot be taught in the classroom but were essential to my dissertation work.

To Sam: thank you for being my sanity, my escape, and my best friend. I am grateful that you were interested enough in bees and butterflies to participate in RMSSN for a second year, as you brought and still bring me so much joy. You helped me through the good times and even got me out of the tougher ones. Thank you for taking time off work to come chase insects when field crews fell through, for seeing the need for my research and the time away from you and home, and for being my R troubleshooter. You always said to me, "We're here for a good time, not a long time," and those words powered me through the rough field days or stressful work weeks. I love you and am so grateful for our bond. Here's to many more bug adventures together in the most beautiful and adventurous places.

Lastly, to the national parks themselves, and those who opted to protect these landscapes for past, present, and future generations. Thank you for inspiring so many people across the world to preserve Mother Earth's greatest treasures, for acting as a playground and place for exploration and science, and for evolving my understanding of the world's most magnificent places. Each park that I have had the privilege to work in is just as special, and it is my moral

imperative to continue protecting these places and the species within them for the greater good.

A lot of things about the state of our planet are uncertain, including within the national parks, but

I hope my research efforts and those of the countless other scientists working in these special

places can stress the importance of conserving these spaces for generations to come.

PREFACE

I caught my first insect (*Danaus plexippus*, a monarch butterfly) back in 2010. I was nearly a teenager and participating in monarch tagging as part of an extra credit assignment for my Advanced Placement Biology class. Growing up in Lawrence, Kansas, I had no idea that my parents had conveniently placed me amongst phenomenal entomology researchers from the University of Kansas, nor the great monarch migration that happens through the Midwest region. As hundreds of butterflies fluttered around my friends and I, we chased down as many as we could to put a small QR sticker on each captured specimen. We giggled at the feeling of butterfly legs on our noses and yelled in frustration at every butterfly that slipped out of our fingers before we could document its presence.

At the time, I did not think much of this opportunity other than that it was cool that we could participate in science outside and see so many butterflies at once. However, this was a core moment in the foundation of my science interests. A few years later, I spent 45 days on a canoe on the Allagash River from Maine to Canada, not catching bugs but rather American bullfrogs and toads. I had just completed my first environmental science class in high school and was starting to make decisions on colleges and potential majors. I had never canoed in my life (I grew up in a landlocked state!), nor caught frogs or toads. Nevertheless, the professors from the College of the Atlantic, the host of this field-based class, made me feel like I belonged. This changed my trajectory towards environmental science and field ecology going into my undergraduate studies, looking into all the possible career opportunities, and imagining what my future could hold.

Starting at Colorado State, I had the vision of becoming a park ranger, but I did not know what this meant. I thought it meant traveling to cool places like Acadia, one of the first parks I visited, and teaching people about science. Meeting Gillian created my poster definition of a park ranger turned professor, and that became my career goal. I still do not know what confidence Gillian saw in me, but she invited me to Hawaii Volcanoes National Park to participate in the 2015 BioBlitz event and needed an entomology student specialist for the trip. With only monarch tagging in my repertoire, I traveled to the Big Island and never looked back.

This story is to say that sometimes, life grants you opportunities that you should not turn down. For many (including even myself at times), the steps needed to pursue a PhD may seem unsurmountable. What got me to this stage of my career are three things: feeling like I belonged in this space because of the trust of advisors and other researchers, a willingness to be uncomfortable and take on an adventure, and luck. Sometimes, a better understanding of yourself means you need to cry on a canoe and feel smelly, underexperienced, and alone. Other times, you may get lucky and discover a new species of dragonfly in a national park. The beauty of being a scientist is that our pathways are never linear and are always changing with the evolution of scientific questions and discovery itself.

I wanted to start my dissertation with this reminder of where I started and now who I hope and will continue to become. Now, I cannot imagine life without an insect net in my hands. Believing in yourself through these hard times takes you farther than the science question itself ever will. So, take the chance! Take the adventure. Learn to say yes, but never regret the no's that need to come up to prioritize yourself. Be proud of what you can accomplish by trusting in yourself, and never let self-doubt get in the way. Life and our career paths are too short to not

pursue what we love. Now, I have a forever love for our parks, our pollinators, and saving our

planet for the greater good.

DEDICATION

This work is dedicated to my family, including Sam. You encouraged me through the hard times

and celebrated the good. I love you all and cannot imagine life without your support.

I also dedicate this work to all who have helped to conserve the national parks – in an uncertain,

changing world, the solace of these special, protected places brings me optimism and peace.

Let's all keep fighting the good fight to save this planet!

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"The parks do not belong to one state or to one section.... The Yosemite, the Yellowstone, the Grand Canyon are national properties in which every citizen has a vested interest; they belong as much to the man of Massachusetts, of Michigan, of Florida, as they do to the people of California, of Wyoming, and of Arizona."

"Who will gainsay that the parks contain the highest potentialities of national pride, national contentment, and national health? A visit inspires love of country; begets contentment; engenders pride of possession; contains the antidote for national restlessness.... He is a better citizen with a keener appreciation of the privilege of living here who has toured the national parks."

-Stephen T. Mather, NPS Director, 1917

CHAPTER 1: INTRODUCTION

Climate change is accelerating worldwide biodiversity loss across all taxa, including insects (Harvey et al., 2023; Díaz et. al., 2020; Sánchez-Bayo & Wyckhuys, 2019). Researchers warn that we are facing an "insect apocalypse" because of climate and land use change (Sánchez-Bayo & Wyckhuys, 2019; Harvey et al., 2023). Biodiversity loss and climate change impact critical ecosystem services such as pollination, an interaction between plants and insects that produces over 70% of global food sources worldwide (Potts et al., 2016). Almost 20% of the most common insect pollinator "flower visitor" functional groups -- bees and butterflies -- face extinction threats within the next generation; however, the patterns and causes of decline are still in question (Potts et. al., 2016).

Many species, including plants and pollinators, are endemic to specific ecosystems; without further conservation efforts, climatic shifts will eliminate existing interactions (Rahbek et al., 2019). These shifts will encourage further non-native species niche partitioning, resource competition, and other unknown detrimental feedbacks (Inouye, 2019). As highly mobile and diverse species, insects have historically been understudied and undervalued, making them more challenging to conserve (Sánchez-Bayo & Wyckhuys, 2019; Harvey et al., 2023). The Endangered Species Act (ESA) of the US includes 97 federally listed insect species; in contrast, 419 vertebrate species are considered threatened or endangered (Entomological Society of America, 2018). The difficulties accredited to insect protection under the ESA include their dynamic relationships with plants that may also have listing status, habitat-specific requirements, and limitations in taxonomic understanding (Harvey et al., 2023; Entomological Society of America, 2018). In some states within the United States (US), insects are not considered wildlife and, as a result, cannot be conserved under laws like the ESA (Einhorn, 2023). With the

knowledge of impending insect decline, yet uncertainties in the conservation next steps, what can researchers and the public do to save these fleeting species?

1. Climate change and pollinator decline

There is evidence that insect populations, the most diverse taxa in the world, are declining due to issues such as climate change, habitat loss and fragmentation, habitat quality deterioration, and other anthropogenic forces (Sánchez-Bayo & Wyckhuys, 2019). Humans depend on insects for critical ecosystem services such as pollination, and without viable populations of bees and butterflies available, over $173 billion United States dollars (USD) worth of human-consumed crops will be lost (Gallai et al., 2009; IPBES, 2016). Because of the heavy reliance on pollinators for ecosystem services and agricultural systems' increasing use of pesticides that have detrimental consequences for pollinator health, some of the fastest rates of insect decline are happening within functional groups such as bees and butterflies (Potts et al., 2016; IPBES, 2016). The patterns of insect decline, as evidenced through historic sampling efforts stored within Natural History Collections (NHCs) and more recent monitoring programs, suggest that pollinator species decline is inconsistent amongst different functional groups (bumble bees versus butterflies) due to shifts in species' ranges, and because of pressures that drive species emergence patterns and life history traits (IPBES, 2016; Sánchez-Bayo & Wyckhuys, 2019).

Pollinator species living in temperate and boreal ecosystems face even greater pressures as seasonal patterns of temperature and precipitation shift, thereby altering current environments (Pörtner et al., 2019). The Intergovernmental Panel on Climate Change (IPCC) projects that shifts in hydrologic and temperature cycles will impact the persistence and migration of species

that are dependent on certain elevational gradients (Pörtner et al., 2019). These patterns align

with the IPCC and the Intergovernmental Science-Policy Platform on Biodiversity and

Ecosystem Services (IPBES) projections that anticipate a greater need for conservation and

adaptation measures to maintain species diversity in areas over time (Pörtner et al., 2019; Pörtner

et al., 2021).

2. Guiding ecological frameworks: resilience, species vulnerabilities, and the panarchy framework

Researchers know that pollinators can adapt to challenges such as climate anomalies, but

the persistence of species, especially those that are resident to the area or have limited range

distributions, faces uncertainty as patterns of disturbance increase in severity (Huan &

D'Odorico, 2020; Adedoja et al., 2018; Carbone et al., 2019). Within plant-pollinator

interactions, researchers predict that species that are resilient to phenological changes will be

more likely to persist than those who will maintain restricted ranges of emergence (Polgar et al.,

2013; Biesmeijer et al., 2006). Resilient species may also include non-native plant or insect

species that could outcompete specialist or native species for floral rewards; however, little data

on the impact of this resource phenomenon has occurred (Giejsztowt et al., 2020).

Ecological resilience refers to the ability of an ecosystem to recover from disturbances or

changes in environmental conditions while maintaining its essential structure and function

(Holling, 1973). This concept is particularly relevant in the context of climate change,

biodiversity loss, and pollinator decline (Winfree, 2013). When biodiversity is lost, ecosystems

become less resilient, making them more vulnerable to further disturbances and changes. One

way to maintain ecosystem resilience is by protecting and restoring critical habitats for species

and ecosystems (Gunderson, 2000). Additionally, efforts to minimize anthropogenic landscape

pressures, such as reducing habitat disturbance or managing invasive species, can all help to enhance ecological resilience and prevent further biodiversity loss. Protecting critical species, such as keystone taxa or those that influence ecosystem services, will also benefit ecosystem resilience (Gunderson, 2000). The broader ecosystem transitions climate change has caused and the adaptive capacity of those species and landscapes experiencing change will have lasting consequences on our planet (Bodin & Wiman, 2004; Gunderson, 2000).

More broadly, panarchy describes the dynamics of complex systems and how resilient or non-resilient systems may overcome environmental feedbacks (Gunderson & Holling, 2002). The panarchy framework emphasizes the importance of interactions and feedback loops between different scales of a system, from individual organisms to entire landscapes (Allen et al., 2014). One of the key insights of the panarchy framework is that ecosystems are constantly adapting and evolving in response to disturbances and changes (Gunderson & Holling, 2002). This process of adaptive cycles involves phases of growth, stability, and reorganization, as well as periods of collapse and renewal. In the context of climate change and biodiversity loss, the panarchy framework stresses that non-resilient systems may collapse or face periods of greater instability (Allen et al., 2014). By understanding patterns of ecosystem adaptation, researchers and land managers can then develop effective strategies for conserving biodiversity and promoting ecosystem resilience.

3. Pollinators and floral phenology shifts

Pollinators act as a good measure of shifts in community structures, including transitions towards ecosystem growth or reorganization, because of their host-plant reliance and vulnerability to habitat quality (Erhardt & Thomas, 1991). As the impacts of climate change—

warmer temperatures, earlier snowmelt patterns, etc.—continue, this will lead to altered community dynamics, such as earlier plant growth and sexual reproduction within spring-blooming angiosperms, earlier emerging insect species, and an increasing risk for detrimental natural disasters (Price & Waser, 1998; Duchenne et al., 2020). Pollinators and plants depend on warmer temperatures and sufficient precipitation for emergence, so climate shifts may encourage desynchrony in behaviors; however, little evidence of this relationship has occurred (Burkle & Alarcón, 2011). Previous studies correlated plant-pollinator phenological mismatches with rising global temperatures, but these studies have been isolated in nature (Bartomeus et al., 2011). Other studies have tracked the evolution of bumble bee species and tongue length as a response to phenological differences, but the evolution of other dependent floral resources did not occur at similar rates, nor were these phenomena tracked amongst other species (Miller-Struttmann et al., 2015). Some researchers have shown that warmer temperatures may negatively affect bumble bees during overwintering (Oyen et al., 2016) or foraging periods (Richman et al., 2020; Pashalidou et al., 2020); on the other hand, climate change may increase periods of activity in other bee species (Bergman et al., 1996). Butterflies have been negatively impacted by the effects of climate change (Forister et al., 2010), and the result of indirect effects through resource availability is also known for this functional group (Boggs & Inouye, 2012).

While these studies articulate the direct and indirect effects of climate change and floral resource availability on bumble bee or butterfly populations, little is known about the importance, connections, or validity of both indirect and direct causes of decline (Ogilvie et al., 2017). Moreover, if plants bloom earlier in the season, and their specialist pollinator species do not coincide with peak phenology, these insects will face greater pressures in locating viable nectaring resources and may need to move upwards in elevation or risk even greater rates of

species decline, while plants will lose genetic diversity from the mismatch of previous, dependent dispersal mechanisms (Thomson, 2010). In addition, different life histories -- queen versus worker bees, or multi-voltinism butterflies -- complicate species presence in relation to plant phenological patterns, and this needs further understanding in relation to species decline and climate change (Forrest et al., 2019). The symbiotic relationship between plants and pollinators, if altered, will have large implications for broader ecosystem structure, function, and resilience.

4. Conservation efforts to mitigate biodiversity loss

In the age of climate change, habitat connectivity through the form of conserved, protected areas may act as one mechanism to mitigate biodiversity loss of all species, including insects (IPCC, 2022; IPBES, 2016). Protected areas are designated spaces where natural ecosystems, wildlife, and cultural resources are conserved and managed for long-term human, species, and ecosystem benefits. Protected areas can help to maintain ecological resilience and provide refugia for rare, threatened, and endangered species. Ecosystems and species can be preserved, despite other land uses and anthropogenic pressures that may occur outside of park borders. (Naughton-Treves et al., 2005). In addition to their ecological benefits, protected areas also offer cultural, recreational, and economic opportunities for people and local communities, which in turn connects people to nature and promotes environmental understanding (Oldekop et al., 2016).

More recently, protected areas have rapidly increased in area on the global scale, with recent initiatives such as the "30 by 30" goal to protect 30% of terrestrial land by 2030 (Saunders et al., 2023). However, it is important to note that protected areas alone are not enough to mitigate biodiversity loss. Habitat or area quantity has not always equated to protection quality,

as researchers warn that protected areas and the species that inhabit these landscapes will still be susceptible to the impacts of climate change regardless of their protected status (Parks et al., 2023; Maxwell et al., 2020; Nascimento et al., 2022). These challenges offer opportunities for policymakers setting conservation targets, researchers studying ecosystem health, and land managers setting protection goals, to collaborate on conservation improvements amidst growing challenges such as climate change. Because of this, protected areas act as opportune study locations to assess the resilience of individual species, communities, and landscape dynamics.

5. Pollinator patterns in international protected areas

The intersection between protected areas, climate change, and pollinator species status has previously received limited attention. International studies indicate that butterfly and bee populations within European national parks have declined by 50% over the past 20 years due to varying causes, including climate and land use change (Hallmann et al., 2017). Researchers in South America predict that future bumble bee range distributions will contract, even amongst protected areas that contain critical habitat for rare pollinator species (Nascimento et al., 2022). In the United States (US), national parks lack comprehensive, long-term biodiversity monitoring programs, especially regarding invertebrate specimens such as insect pollinators (Shafer, 1999; Sánchez-Bayo & Wyckhuys, 2019). Historically, shifts in species range on the global scale have been observed and documented using museum and herbarium collections; however, the amount of information transcribed to track phenological shifts in specimens, both in the field and within NHCs, is limited within the US (Polgar et al., 2013; Price & Waser, 1998). Due to the insufficient pollinator datasets available within the National Park Service (NPS), monitoring projects such as those undertaken by Hallmann et al. (2017) have historically not occurred.

6. Climate change in United States National Parks

Within the United States Rocky Mountain region, high elevation areas have documented climate pressures, including increasing temperatures and rapid glacier retreat. Protected areas within the Rockies have also documented dramatic losses in snowfall accumulation and earlier spring flooding (Romme, 1982). Two protected areas in the Rocky Mountains, Yellowstone (YELL), and Grand Teton (GRTE) National Parks, have documented climate change impacts with earlier spring emergence of hibernating animals and earlier plant phenology patterns (Middleton et al., 2013; CaraDonna et al., 2014), while also facing major, 1000-year fires in the past 30 years. The area has projected summer temperatures increasing by 3°C under RCP4.5 (stabilization scenario), and up to 8°C under RCP8.5 (business as usual scenario) by 2100 (Pörtner et al., 2022; Hostetler et al., 2021; Westerling et al., 2011). These values are higher projections than the global RCP mean predictions (1.8°C for RCP4.5 and 3.7°C for RCP8.5) (Pörtner et al., 2022). The area is expected to lose nearly half of its current seasonal snowpack, almost 40% of its June-August runoff, and face an increased transition (10%) of precipitation from snow to rain, all by 2100 (Hostetler et al., 2021).

In addition, the boundaries of Yellowstone and Grand Teton are contained within the Greater Yellowstone Ecosystem (GYE), an 890,000-hectare area that is the most connected, temperate-zone ecosystem conserved within the continental United States (Yellowstone National Park, 2022.). GYE land management agencies work together on regional issues and have documented shifts in plant, invertebrate, and animal communities in response to climate change occurring in and beyond the national parks (Hansen & Phillips, 2018). Because of its rich conservation goals towards habitat connectivity and biodiversity protection (Noss et al., 2002), as well as the pressing need to better understand resources for priority protection (Yellowstone

National Park, 2022), the GYE acts as a model ecosystem to assess the biodiversity vulnerability of nearly any taxonomic group in the age of climate change.

7. Previous phenology and pollinator efforts in Grand Teton and Yellowstone

Climate shifts in GRTE and YELL have and will continue to affect species patterns, including plant phenology, resource availability, and pollinator emergence patterns. More recently, researchers such as Bloom et al. (2022) found that first flowering time in GRTE has advanced since the 1970s, and this could result in pollinator emergence shifts over time as well; however, these direct relationships have not been studied in the GYE. In contrast, a review of changes in spring onset (both first leaf and bloom index) across all natural resource national parks found that YELL and GRTE had "no extremes" between historic and current phenology trends (Monahan et al., 2016); this indicates opportunities for additional data analyses to understand patterns of change.

Insect decline, as far as it can be detected, may occur in national parks like GRTE and YELL where common drivers of decline, such as habitat conversion and other anthropogenic pressures, are not as prevalent. However, other potential causes of decline, such as invasive plant control through pesticide use, do occur (Olliff et al., 2001; Stohlgren et al., 2013). Both parks have previous research efforts tied to butterflies and bees that enable researchers to address questions such as the effect of climate change on pollinator species over time (Bowser, 1988; Lutz, 1989; Bagdonis, communication via C.P. Gillette collections; Opler, communication via C.P. Gillette collections; Auckland et al., 2004; Dillon, 2011; Gompert et al., 2010; Rykken et al., 2014). Through field experimental set-ups, previous climate change and pollinator research by Debinski et al. (2014) indicated strong effects of passive heating and snow removal on the

nectar content of floral resources used by *Parnassius* butterflies. While these datasets provide an understanding of occurrence records, recent large-scale sampling initiatives to understand the status of all butterfly families and bumble bees have not occurred, nor in connection with other datasets such as climate variables or floral phenology patterns.

8. The data digitization era: virtual collections and citizen science applications

With stronger technological tools, researchers can bridge topics such as climate change, floral phenology, and pollinator diversity using dynamic, growing tools such as virtual datasets and citizen science to address conservation questions while minimizing lethal sampling efforts and increasing data availability. More recent introductions of large-scale datasets through citizen science, where the public contributes toward scientific efforts (Bonney et al., 2009), have the potential to elucidate species patterns of decline (Forister et al., 2021), in addition to the use of NHCs and other research efforts. Emerging mobile phone technology has increased the collection and distribution of citizen science datasets, and with improvements to taxonomic and locational accuracy since their inception (Mazumdar et al., 2018). By complementing data sources from taxonomic experts and community scientists, species assessments can be done during the age of NHC database digitization (Biodiversity Collection Network, 2019) and with the assistance of increased public participation in the scientific and biodiversity collection processes (Bonney et al., 2009). Given the historic data availability for GRTE and YELL, as well as current NPS-wide citizen science efforts to better understand park biodiversity (*National Park Service*, n.d.), these data sources can be applied to bumble bees and butterflies to understand the status of species amongst GYE landscape changes. Museum resources digitized within virtual repositories on a national level can be used to assess the nature of available data, such as shifts in

species emergence, range, and functional traits of bumble bees and butterflies, so that a broader perspective of historical data is understood.

US national parks have previously supported citizen science sampling efforts such as the Backyard Christmas Bird Count, all-taxa biodiversity inventories in parks such as the Great Smoky Mountains, the National Fourth of July Butterfly Count program, and National Phenology Network floral assessments housed within the Nature's Notebook platform (Swengel, 1990; Bloom et al., 2022). These projects are some of the most critical data sources for tracking biodiversity changes within US protected areas (Bonney et al., 2009; Bonney et al., 2014). Pollinator-specific citizen science efforts have happened within other US protected areas such as the North Cascades, Mount Rainier, and Great Smoky Mountains National Parks (Rochefort & McLaughlin, 2017; Scholtens & Wagner, 2007), through the BioBlitz program affiliated with National Geographic and the California Academy of Sciences (Lundmark, 2003), and with assistance from national history museums such as the Smithsonian Institution (Clark & Clark, 1951). Citizen science datasets will continue to become richer in both data quality and quantity for both the parks and researchers as technology improves and public interest in scientific discovery grows (NAS, 2018). While citizen science does present some limitations, such as the types of questions that can be asked by a researcher (Ellwood et al., 2017), the effort (and funding) required to successfully implement community help and long-term engagement (Bonney et al., 2014), data biases, and data accuracy (Lukyaneneko et al., 2016; Aceves-Bueno et al., 2017), these limitations are outweighed by the long-term benefits of such data collection and its ability to provide understanding to current data gaps within the parks.

9. Research motivations and dissertation organization

Through this research, I intend to answer critical questions on the status of pollinator biodiversity within the GYE by combining virtual and field-collected datasets tied to climate, floral phenology, and pollinator species occurrence, all of which can provide evidence towards bumble bee and butterfly species' resilience in the age of the GYE's changing climates and habitats. My passion for insects started through participation in the National Park Service (NPS) BioBlitz program at Hawaii Volcanoes National Park in 2015. BioBlitzes allowed parks to assess species biodiversity within a 24-hour time period using citizen science. While BioBlitzes were never intended to determine the rate of biodiversity loss or the effect of climate change on species found within the parks, these rapid species inventories acted as mechanisms for parks to identify lesser-known taxa, engage with local communities and taxonomic experts, and promote natural and cultural resource understanding (Baker et al., 2014). As a novice entomologist myself, the BioBlitzes opened new doors to data discovery and public engagement within special places like the national parks, and it became a transformative experience in shaping my research interests. I quickly learned that national parks, despite their long history of resource preservation, have limited understanding of lesser-known taxa such as insects, and this knowledge gap continues today (Shafer, 1999; DeVivo, 2019).

In 2018, I began my graduate studies on pollinators within GRTE and YELL. Much like my previous research experience, I opened new doors to data discovery and taxonomy while working in two of the world's most renowned and intact temperate ecosystems (Yellowstone National Park, 2022). Unlike Hawaii Volcanoes, GRTE and YELL had historic pollinator datasets I could build upon to inform research questions, including my advisors' own studies (Bowser, 1988; Lutz, 1989; Bagdonis, communication via C.P. Gillette collections; Opler,

communication via C.P. Gillette collections; Auckland et al., 2004; Dillon, 2011; Gompert et al., 2010; Rykken et al., 2014). Additionally, I could apply previously used research tools, such as citizen science and virtual data applications, to my studies while contributing to the general understanding of insect taxa in the west. My motivations for doing work in these parks became multifaceted in nature, and I continued to uncover more questions than answers. As I collected hundreds of bumble bees and butterflies, I noticed landscape changes occurring simultaneously: changes such as the driest, warmest seasons in the GYE's record, extreme weather in the form of mid-summer cold snaps and snow, and landscapes changed in the short and long term by wildfires (Hostetler et al., 2021). I also noticed patterns of species resilience amongst these landscape changes, while also observing species facing rapid rates of decline (Graves et al., 2020; Janousek et al., 2023).

These experiences act as my motivation to determine the impact of climate change on pollinator biodiversity within the GYE. My innate curiosity, to first establish the status of species diversity in the parks, but also with the intrinsic drive to contribute towards broader insect conservation efforts, guided my dissertation research and the subsequent questions. Broadly, I seek to define the status of pollinator species understanding for the area and how landscape dynamics, such as changing climates and resource availability, may impact species diversity. This dissertation hopes to inform researchers and park managers on the status of pollinator data understanding and species behavioral patterns within the parks, a research avenue that requires greater attention as biodiversity loss and climate change pressures are amplified in the future. Protected areas may act as some of the last reservoirs of species diversity, and they may be shielded from other human causes of species decline such as habitat deterioration, agricultural intensification, and other land-use change (IPCC, 2022; IPBES, 2016). As such, the GYE acts as

a model landscape to address the state of pollinator biodiversity amidst a changing climate, given its rich conservation goals, historic data understanding that, in contrast, is more robust compared to other park landscapes, yet evident climate change effects.

Pollinator research creates a unique tie between climate data and biodiversity changes within protected areas. The close relationship between pollinators and flowering plants mirrors climate shifts and widespread biodiversity change happening on a global scale (Pörtner et al., 2019; Potts et al., 2016). Historic floral phenology and pollinator patterns can be documented through NHCs, citizen science, and virtual datasets, as well as in research projects conducted within the parks. These connections between datasets have yet to be studied within the GYE. Citizen science efforts, along with new technological tools, have only increased the data available on insect pollinators, especially for bumble bees and butterflies, and such datasets are less taxonomically complex than other pollinator groups, such as flies, beetles, and other insects that perform important pollination functions but require more taxonomic expertise to accurately document (Kremen et al., 2011; Dillon, 2011).

The following questions serve as guidance for this research.

1. How do bumble bees and butterflies respond to climate change effects, such as changes in temperature, precipitation, snowpack, and ecosystem disturbances (i.e., wildfire)?

2. What pollinator species (bumble bees and butterflies) were known or documented to occur within the GYE from 1900-2021, and what patterns are observed within virtual databases regarding digitization and species understanding efforts?

3. How have GYE floral resources shifted in phenological timing, if at all, and what is the relationship of both pollinator occurrence and phenological trends to observed temperature and precipitation changes?

Systematic pollinator monitoring that accurately tracks these questions within protected areas requires: A) consistent sampling measures on a national level that are focused within rapidly changing landscapes such as temperate ecosystems; and B) a synthesis of the current, historical, citizen science-collected, and phylogenetic records available for each region (Vanbergen & The Pollinator Initiative, 2013). This is especially important as recent climate and land-use changes have been followed by pronounced biological responses from plants and pollinators, including phenological changes, range shifts, and an increasing diversity of generalist and non-native species while more specialized and resident species decline (Algar et al., 2009).

This dissertation is designed as three separate studies with overlapping themes centered broadly around pollinator (bumble bee and butterfly) communities, climate change, and species responses. Ecosystem and species resilience and the panarchy framework served as the primary ecological frameworks for these studies. The first study provided the background for global patterns of species responses to climate change effects using a meta-analysis approach. While the effects of climate change may not be felt by species in GRTE and YELL currently, the GYE may become less resilient as an ecosystem over time, and nationally and internationally observed species responses may become more apparent. Through this study, I argued that researchers need to articulate the complexities of species patterns and their subsequent responses to changing landscapes in more detail. The second study established a baseline understanding of the species diversity known to the parks and how virtual repositories reflect the taxonomic biases present within entomology datasets towards charismatic or unique taxa. Nonetheless, this chapter acted as the foundation for species diversity knowledge that could inform gaps in previous GYE research efforts. The third study applied research understandings from the previous chapters to

field datasets with a focus on plant-pollinator phenology relationships. This study helped to inform the status of pollinator species and their responses to changing climates in the parks through their indirect and direct relationships with landscape changes and resource availability. The final chapter summarizes my findings through lessons learned, suggested future research avenues, and three species case studies based on my results. These species case studies act as recommendations for species to prioritize in conservation efforts, data collecting and reporting, and in consideration of additional management priorities that the parks face, such as managing for invasive species.

All chapters relied on tools or technology available at one's fingertips and using citizen science, digitized museum collections, and long-term climate and phenology monitoring datasets. My research used citizen science as a collection tool to make data accessible while minimizing resource impacts and ensuring accurate species identifications. As a result, other researchers or the public can utilize my observations for their own scientific discoveries. Field crew participants were considered citizen scientists and novice entomologists, but their data contributions and project co-creation required more active engagement in the project than most citizen science efforts require of their participants (Shirk et al., 2012; Whipple et al., 2022a). The underlying theme of data tools and technology observed across my research attempted to demystify the resources necessary to answer biodiversity and landscape-level ecological questions. At the same time, the museum collection data and additional data repositories established within the parks strengthen the results of this research, and I must acknowledge these research foundations upon which I can build using new tools and technology. As such, these data mechanisms are highlighted when relevant across the respective studies.

CHAPTER 2, STUDY 1: POLLINATOR BIODIVERSITY IN THE ANTHROPOCENE: A META-ANALYSIS OF OBSERVED PHENOLOGY-POLLINATOR SHIFTS IN RESPONSE TO CLIMATE CHANGE

1. Summary

Climate and land-use change are arguably two of the largest drivers of biodiversity loss worldwide. However, pollinator species patterns, whether leading to a beneficial or detrimental population response, are less clear, and there are uncertain amounts of confidence and evidence to back such claims. Here, we analyze the available literature for two pollinator groups, bumble bees and butterflies, to understand species responses to changing climate and land-use variables. Using a meta-analysis approach, we found 22 bumble bee and 113 butterfly-relevant studies that found changes in patterns and behaviors such as species emergence, range distribution, richness, and abundance. While the available literature relevant to bumble bees was limited, there is high confidence that the group is facing earlier emergence and phenological mismatches with floral resources, in addition to decreases in populations and range distributions. Butterfly literature was more available but did not yield greater confidence in species responses; evidence, however, does align in changing species emergence patterns, range distributions, and amongst generalist versus specialist groups. This study can inform future biodiversity/climate change research priorities for a highly diverse taxonomic group such as bees and butterflies, particularly in areas with mixed data availability and species understanding.

2. Introduction

2.1 Biodiversity loss and climate change

Researchers state that climate change will be one of the most significant anthropogenic drivers of future biodiversity loss, but the rate at which species decline due to changes in temperature, precipitation, and extreme weather patterns varies based on regions and species

resilience (IPBES, 2016; Trisos et al., 2020; Moritz & Agudo, 2013; Richman et al., 2020; Bellard et al., 2012). Under the business-as-usual emissions scenario RCP 8.5 (Representative Concentration Pathway), 81% of terrestrial species assemblages are expected to be exposed to unprecedented warming before 2100, which will have detrimental effects on species persistence to the point of irreversible tipping points of survival and system collapse (Pörtner et al., 2019; Moritz & Agudo, 2013; Trisos et al., 2020). In the age of climate change, a better understanding of the intersections of historical and current biodiversity data and how changing climate variables impact species diversity is needed to further predict the rates of species change that may occur.

2.2 Pollinators and climate change

The impact of temperature warming, changing precipitation levels, and a decrease in snowpack has had mixed effects on pollinator species across the world: some species have been able to adapt and shift their range or establish in new areas as spring and summer seasons lengthened, whereas many species have risked population declines due to impending pressures such as habitat loss, decreased thermal tolerances, and resource competition (Pörtner et al., 2019; IPBES, 2016; Miller-Struttmann et al., 2015; Chen et al., 2008; Makino et al., 2019; Soroye et al., 2020; Britten et al., 1994). Researchers know that pollinator species are sensitive to temperature and precipitation fluctuations; for bumble bees, climate thermal limits can exceed the physiological thermal limits of the species, thereby leading to range shifts or declines in species richness (Soroye et al., 2020). Butterflies are equally dependent on temperature to break diapause and obtain nectar and larval resources from their host plants, and increasing temperatures in conjunction with drought conditions can have negative effects on

metapopulation persistence (McLaughlin et al., 2002). Additionally, researchers know that pollinators can adapt to challenges such as climate anomalies, but the persistence of species, especially those that are resident to the area or have limited ranges in elevation, faces uncertainty as patterns of disturbance increase in severity (Huan & D'Odorico, 2020; Adedoja et al., 2018; Carbone et al., 2019). These species-landscape dynamics may lead to range restrictions, altitudinal and latitudinal migrations, species declines, and even species extinctions.

However, climate change variables are not always the direct cause of a pollinator's response: because pollinators rely on floral resources for survival, the direct effect of changing climates on floral emergence and abundance may be more significant than the impact of climate change on pollinator presence itself (Ogilvie et al., 2017; Carbone et al., 2019; Huang & D'Odorico, 2020; Richman et al., 2020). The Intergovernmental Panel on Climate Change (IPCC) projects that regardless of the RCP, 10-40% of mean snowpack worldwide will decrease from 2031-2050, and if following the RCP 8.5 scenario, snowpack will decrease 50-90% (Pörtner et al., 2019). For pollinator species dependent on early emerging spring flowers, which rely on snowpack melt to bloom, earlier trends of snowpack decline from a seasonal perspective will shift floral phenological patterns and may restrict floral resource availability over time (Ogilvie et al., 2017; Inouye, 2019; Duchenne et al., 2020). Nicholson and Egan (2019) argued that, by combining temporal and spatial mechanisms such as climate-driven range shifts in relation to shifts in floral phenological patterns, this would ensure that predictions towards pollinator decline are more accurate in the species response. This relationship should be studied in more detail, especially in comparison between species resource generalists and specialists, as well as between univoltine (single-generation producing) and multivoltine (multiple-generation producing) species (Bartomeus et al., 2013; Miller-Struttmann et al., 2015).

2.3 Study goals

While the impacts of warming may have a mixed response on the persistence of plant and insect species worldwide, the certainty of individual species' reactions to changes in climate are relatively unknown. Species can be preserved through conservation and adaptation measures on a global scale, as well as with growing networks of protected areas focused on preserving critical ecosystem services like pollination (Pörtner et al., 2019). However, more information is needed on the dynamics between climate change and pollinator species resilience, species' responses to future climate variation, and the impacts of anthropogenic disturbances on pollinator species diversity over time (Makino et al., 2019; Lever et al., 2020; Huang & D'Odorico, 2020; Nicholson & Egan, 2019; Dorenlas & Daskalova, 2020). Researchers need to better understand those species who will be most vulnerable to climate change, as well as those that may thrive under altered land and climate scenarios (Bartomeus et al., 2013). Because international organizations such as the IPCC know that changes to ecosystems due to anthropogenic forces have affected seasonality, species abundance and distribution, ecological disturbances, and overall ecosystem functioning, it is critical to document current changes happening on an ecosystem-level, relate these effects back to historical species distributions, and project trends reflecting ecosystem health for the future (Pörtner et al., 2019; Johnson et al., 2011). This will help in determining ecosystem and individual species resilience towards changing climates (Holling, 1973), as well as those species for which stronger conservation measures may need to occur to prevent irreversible feedback loops (Gunderson & Holling, 2002).

Due to these uncertainties present in the literature on pollinators and climate change, this research consolidates previous studies on bumble bee and butterfly species richness, abundance, emergence, and distribution responses to climate variation to inform researchers on taxon

sensitivities to changing landscapes, and behavioral strategies to observe within future climate/pollinator species studies. The cause and rate of pollinator decline tied to climate change are undefined metrics, and this research specifies such responses and the agreement of such patterns that are found within the literature.

The following question guided this research: how do bumble bees and butterflies respond to climate change effects, such as changes in temperature and precipitation? I hypothesize that climate change (i.e., temperature and precipitation change) is negatively altering the range distributions, species emergence, richness, and abundance of pollinators. Out of all the impacts of climate change, I hypothesize that temperature has had the most significant effect on species responses. I also hypothesize that species with specialized habitat and/or plant preferences are declining at higher rates than generalist/non-native species due to warmer temperatures. However, the specific nature and extent of these responses will likely vary among pollinator species, depending on their physiological characteristics, regional distribution, and resource preferences. By synthesizing species patterns tied to climate change, this research provides clear evidence of pollinator behavioral and distribution patterns, including evidence of species that may be resilient to changing climates and those that are most vulnerable.

3. Methods

3.1 Literature review

To collate all published articles with relevance to climate change impacts on bumble bees and butterflies, I used a variation of search terms in the Web of Science literature repository. These included the following: bumble bees AND climate change*; bumble bees AND global change*; bumble bees AND temperature warming*; bumble bees AND precipitation *; bumble

bees AND global warming*; bumble bees AND snowpack*; bumble bees AND fire*; butterflies AND climate change*; butterflies AND global change*; butterflies AND temperature warming*; butterflies AND precipitation *; butterflies AND global warming*; butterflies AND snowpack*; butterflies AND fire*. Boolean phrases ensured that results included research related to both search terms, and the asterisk ensured that words with different endings (such as fires, global changes, etc.) appeared as well.

The inclusion criteria for this meta-analysis followed the population, treatment, control, and outcome (PTRO/PICO) framework (Huang et al., 2006). The populations of concern included bumble bees (order Hymenoptera, genus *Bombus*) and the butterfly order (Lepidoptera). In the analysis, populations were not limited to North America, given the predicted amount of literature available. The treatments of relevance included studies with experimental or manipulated climate effects, observational studies, and modeled projections; the literature considered for this analysis required some combination of climate driver, floral phenology, and/or pollinator response data attributes. The outcomes of interest included species responses to climate effects, either in the form of richness, abundance, emergence, or distribution patterns (direct responses to climate change) and/or evidence of plant-pollinator phenological responses (indirect responses to climate change). For butterflies, species generalists versus specialists and their responses to climate variables were also tracked. Life stage and generational trends were tracked for both bumble bees and butterflies. For bumble bees, the differentiation was made between queens and workers, and for butterflies, the difference was made between univoltine and multivoltine species. Studies were omitted if they were not considered primary literature, such as reviews, meta-analyses, editorials, or commentaries. Additionally, publications that were

found as results within Web of Science but ended up having no institutional access from Colorado State University were omitted.

3.2 Meta-analysis data analysis

Each species response received an evidence and agreement statement to indicate the confidence level of certainty for the projected species response (Mastrandrea et al., 2010). Both variables followed the Intergovernmental Panel on Climate Change (IPCC) guidance for addressing scientific certainty in high-level research reviews. Results with greater than 90% species response agreement were considered "high confidence," while those with 70-89% and 50-69% were considered "medium" and "low confidence." Results with less than 50% agreeance were considered "very low confidence." Evidence of more than 30 publications were considered "robust evidence," while those between 10-30 publications were considered "medium evidence," and fewer than 10 publications were considered "limited evidence."

Based on the evidence and agreement results, data from both bumble bee and butterfly studies were then grouped into publications measuring the same species responses. These included organization into species phenology (indirect) and population/distribution (direct) categories. Then, to test if bumble bee and butterfly response patterns to climate variables were similar, I performed one-tailed t-tests amongst each species group and their observed responses/changes, followed by Welch's unequal variance t-tests to compare the difference in bumble bee and butterfly responses for each category (Welch, 1938). T-tests were run for all species response categories, with four or more publications available for each taxonomic group.

Last, to explore these responses more specifically in relation to climate variables, I performed multivariate statistics in the form of principal component analyses (PCAs) amongst

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publications measuring similar climate variables and species responses. Both bumble bees and butterflies were grouped together in these analyses, and study areas were standardized by regional locations. Publications with missing values for the four common response variables were not included in the PCA; consequently, this eliminated publications and their results from the final analysis. PCA analyses and plots were completed using the R packages "FactoMineR" (Husson et al., 2016), "factoextra" (Kassambara & Mundt, 2017), and "corrplot" (Wei et al., 2017).

4. Results

4.1 Meta-analysis trends

Web of Science results yielded 319 bumble bee and 3,638 butterfly articles. After refining articles based on relevancy, institutional access, and experimental metrics, 22 bumble bee and 113 butterfly articles were used in this analysis (Figure 1.1). Bumble bee trends came from 60 countries and seven US states, while butterfly trends came from 61 countries and 30 US states. There was a predominant focus on taxon-wide studies across both bumble bee (18 taxon-wide; four species-specific studies) and butterfly (81 taxon-wide; 32 species-specific studies) literature. The exceptions included a few articles that highlighted species known to be rare or in decline (i.e., *Danaus plexippus*, monarch; *Speyeria idalia*, regal fritillary; *Bombus funebris*, gray-backed bumble bee), or the dominant/charismatic species observed within an ecosystem (*Parnassius apollo*, Mountain Apollo; *Pieris rapae*, Cabbage White). For bumble bees, the most common climate variables studied included temperature (36% of articles), fire (18%), and snowmelt date (14%). For butterflies, the most common climate variables studied included temperature (47% of articles), the combination of temperature and precipitation (24%), and fire

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(15%). For article information, including study taxa and location, see Appendice A1 (bumble bees) and A2 (butterflies).
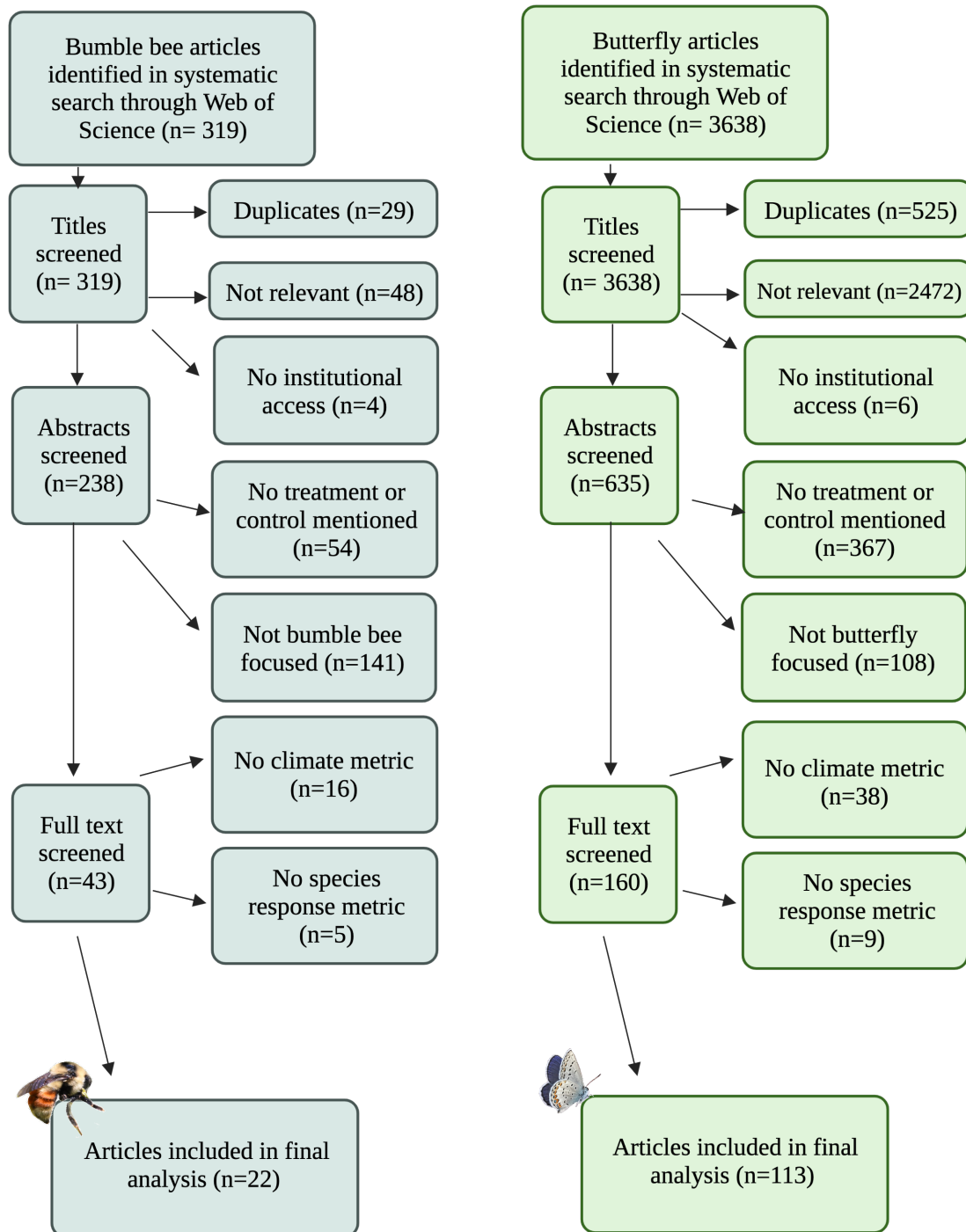
Figure 1.1. Flow chart identifying relevant literature for the species-climate response meta-analysis. Based on data metrics, 22 bumble bee and 113 butterfly papers were used for the analysis. Figure created with BioRender.com.

4.2 Evidence and agreement trends

The evidence and agreement statements for each species response to climate variables are reported in Tables 1.1 and 1.2. For bumble bee studies, earlier plant phenology, generational or life cycle emergence changes, and overall species emergence shifts were responses with medium- to high-confidence, but there was limited evidence available (Table 1.1). Butterfly literature observed medium- to high-confidence earlier trends in categories such as species emergence and plant phenology emergence patterns, and these categories had medium- to limited- evidence. Changes in univoltine and multivoltine species generations indicated earlier, additional generation occurrences; however, this species response only had limited evidence. Because of the available evidence and agreement, species emergence was the indirect response variable further analyzed in this study.

Table 1.1. Evidence and agreement statistics indicating phenology and life stage species responses to climate variables for papers used in the meta-analysis (n=22 papers for bumble bees and n=113 for butterflies). Dark gray boxes indicate high confidence (>90%), medium gray boxes indicate medium confidence (70-89%), light gray boxes indicate low confidence (50-69%) and white boxes indicate very low confidence (<50%) in the species response. Italicized percentages indicate medium evidence (10-30 publications); underlined percentages indicate limited evidence (<10 publications).

	Phenology/Species Emergence Trends	**Species Emergence**	**Plant Phenology/ Emergence (Phenological Mismatch)**	**Generations/Life Cycles**
Bumble Bees	Late	25%	0%	0%
	Early	75%	100%	100%
	Uncertain effect	0%	0%	0%
Butterflies	Late	9%	0%	50%
	Early	*78%*	100%	17%
	Uncertain effect	13%	0%	33%

Within the population and distribution species responses (Table 1.2), bumble bees trended towards decreases in richness but increases in species abundance; both responses were considered low confidence and had limited evidence. Bumble bee range contractions and overall population changes in response to climate variables were most widely agreed upon in the literature, with 67% of studies indicating increases in populations, and decreases in species range distribution (contractions). Butterflies had mixed responses in species richness and abundance trends, with all trends having very low or low confidence and limited to medium evidence. The most prominent responses included decreases in species abundance (medium evidence) and increases in species generalists' (limited evidence). Much like the bumble bees, 67% of butterfly studies have also observed species range contractions. Because of the available evidence and agreement, species richness, abundance, and range distribution were the direct response variables further analyzed in this study.

Table 1.2. Evidence and agreement statistics indicating population and distribution species responses to climate variables for papers used in the meta-analysis (n=22 papers for bumble bees and n=113 for butterflies). Light gray boxes indicate low confidence (50-69%) and white boxes indicate very low confidence (<50%) in the species response. Italicized percentages indicate medium evidence (10-30 publications); underlined percentages indicate limited evidence (<10 publications).

		Response	Richness	Abundance	Population Change	Specialist Change	Generalist Change	Range
Bumble Bees	Population Responses	Increase Effect	33%	55%	67%			
		Decrease Effect	50%	18%	33%			
		Uncertain Effect	17%	27%	0%			
	Distribution	Expansion						33%
		Contraction						67%
		No Change						0%
Butterflies	Population Responses	Increase Effect	47%	31%	34%	22%	56%	
		Decrease Effect	29%	50%	45%	33%	19%	
		Uncertain Effect	24%	19%	21%	39%	25%	
	Distribution	Expansion						15%
		Contraction						67%
		No Change						17%

4.3 Species response trends

Based on the available data, changes in species emergence, richness, abundance, and range distribution were compared amongst bumble bees and butterflies (Table 1.3; Figure 1.2). Both bumble bees and butterflies have observed changes in emergence days, with bumble bees emerging on average 9.75 days earlier and butterflies emerging 8.34 days earlier (Figure 1.2 A); the butterfly emergence changes observed amongst publications were considered significant

(p<0.0005). Bumble bee (-2.74) and butterfly (-0.82) richness have declined (Figure 1.2 B),

while bumble bee abundance increased (341.9) and butterfly abundance decreased (-11.06)

(Figure 1.2 C); both responses were considered non-significant. The changes in range

distribution also varied between species; bumble bees have seen an average range contraction of

nearly 10%, while butterflies have seen a significant range contraction of 25% (p<0.004) (Figure

1.2 D).

Table 1.3. One-tailed t-test bumble bee and butterfly responses, and Welch's unequal variance t-test comparing species responses. P-values <0.05 denoted with * and are considered significant. Butterfly species emergence responses and changes in species distributions were significant.

	Species Emergence (Days Early (+) / Late (-))					
	t	df	p-value	Lower 95% CI	Upper 95% CI	Mean
Bumble Bee	2.08	3	0.13	-5.2	24.7	9.75
Butterfly	4.09	22	0.0005*	4.11	12.56	8.34
Bumble Bee/Butterfly	0.28	4.22	0.8	-12.519	15.35	-
	Richness (# Unique Species)					
	t	df	p-value	Lower 95% CI	Upper 95% CI	Mean
Bumble Bee	-1.6	5	0.17	-7.15	1.67	-2.74
Butterfly	-0.45	36	0.66	-4.57	2.92	-0.82
Bumble Bee/Butterfly	-0.76	19.61	0.46	-7.19	3.35	-
	Abundance (Total # Species)					
	t	df	p-value	Lower 95% CI	Upper 95% CI	Mean
Bumble Bee	1.57	10	0.15	-144.47	828.28	341.9
Butterfly	-1.35	25	0.19	-27.89	5.77	-11.06
Bumble Bee/Butterfly	1.62	10.03	0.14	-133.56	839.49	-
	Changes in Species Distribution Range (%)					
	t	df	p-value	Lower 95% CI	Upper 95% CI	Mean
Bumble Bee	-0.61	3	0.58	-53.39	36.13	-8.63
Butterfly	-3.2	23	0.004*	-41.63	-8.91	-25.27
Bumble Bee/Butterfly	1.03	5.13	0.35	-24.52	57.81	-
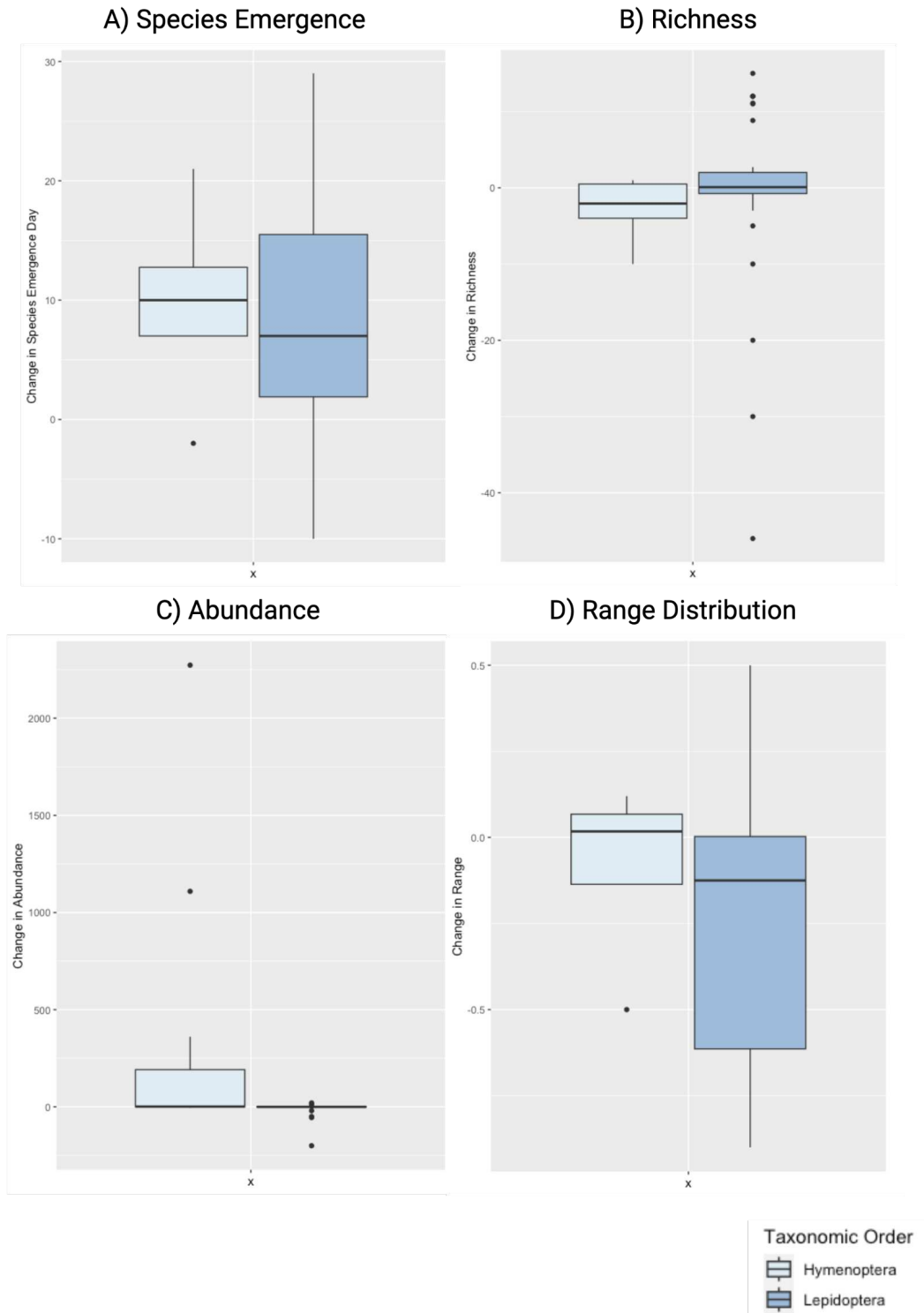
Figure 1.2. Bumble bee (order Hymenoptera) and butterfly (order Lepidoptera) species responses, including change in emergence day (A), change in richness (B), change in abundance (C), and change in range distribution (D). Butterfly responses (dark blue) were more spread out, except for within the abundance category (C). Bumble bee responses (light blue) were more similar, except for within the abundance category (C), where strong outliers occurred.

4.4 PCA trends

Given the availability of data, the PCAs focused on temperature changes and their response on species emergence, richness, abundance, and range distribution. PCA plots for bumble bee and butterfly trend data highlight the representation quality of variables as well as the correlation between species responses and temperature variation (Figure 1.3). Within the species emergence dataset, temperature change and species group (bumble bees versus butterflies) had strong, negative correlations with one another; on the other hand, species emergence changes and study regions were positively correlated (Figure 1.3 A). All species emergence variables were well represented within the PCA, with quality of representation values above 75%. The species richness dataset saw correlations between changes in richness and the study regions and between species groups and temperature changes (Figure 1.3 B). Species groups and temperature changes had the highest quality of representation values, with both variables above 70%. The abundance dataset saw correlations between study location and species group and a slight negative correlation between study location, species group, and changes in abundance; temperature change, however, had the highest quality of representation value at nearly 100% (Figure 1.3 C). Within the distribution dataset, temperature change and species groups were negatively correlated, and the study region and range distribution change were also negatively correlated (Figure 1.3 D). Temperature change and range distribution change had the highest quality of representation values, with both variables at 75%.
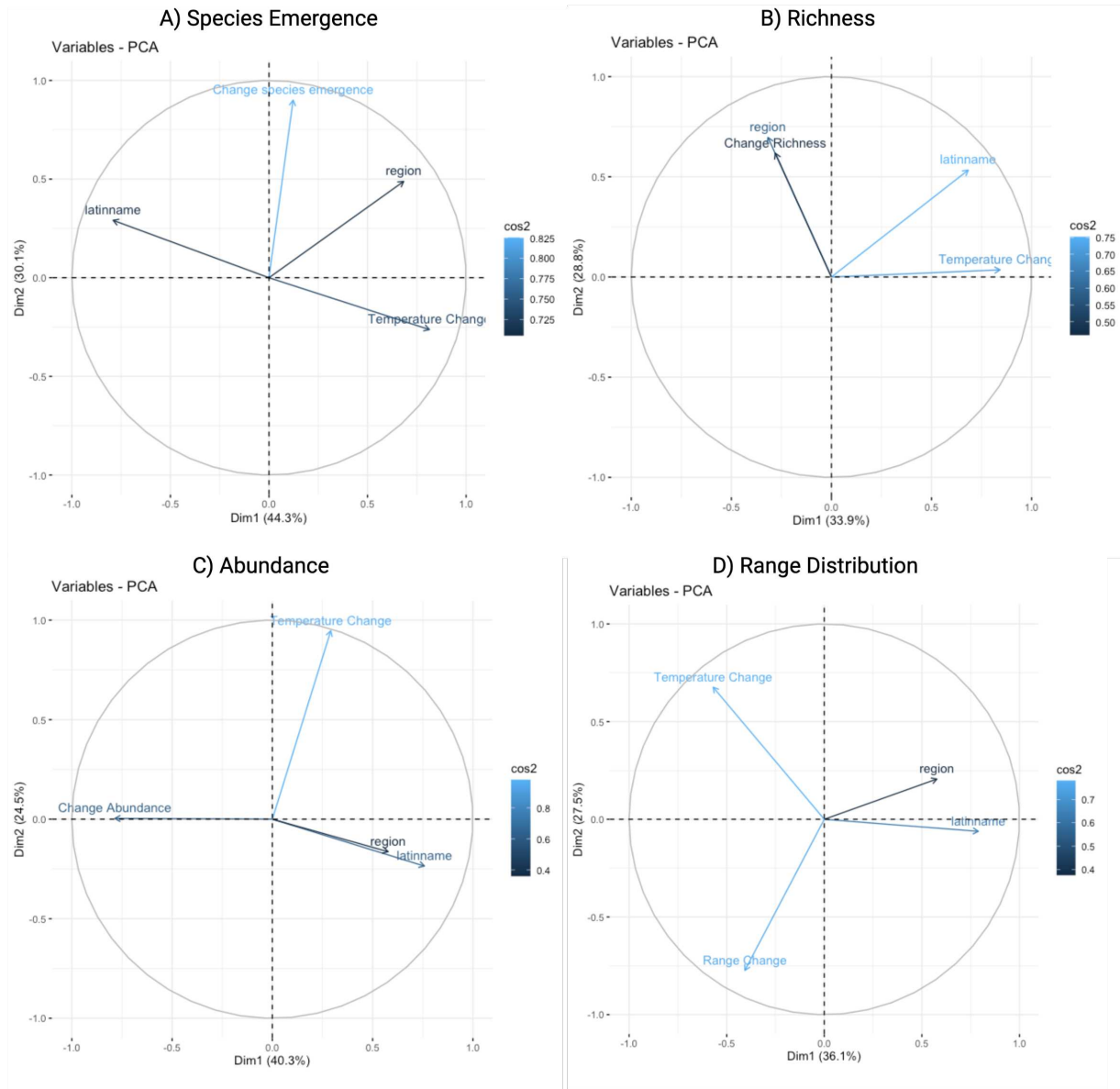
Figure 1.3. PCA correlation plot representing bumble bee and butterfly change in emergence (A), change in richness (B), change in abundance (C), and change in range distribution (D) responses in relation to temperature variation. Positively correlated variables are grouped together, whereas negatively correlated variables oppose each other along the plot origin (ex: region and range change). Arrows further away from the origin represent strong variable representation; those closer to the origin represent weak variable representation.

The PCAs validate the correlation of species responses to climate changes. For species

emergence (Figure 1.3 A), the negative correlation between temperature and taxonomic groups

aligns with the rate of change occurring within species' groups; butterflies, on average, have emerged one day later than bumble bees, yet the 95% confidence interval for bumble bees ranged from five days late to 24 days earlier. Temperature and its effect on species emergence, as a result, have not responded similarly across the two species groups. For all response categories, study regions were important to consider, as regional variation had positive correlations with species emergence (Figure 1.3 A) and richness changes (Figure 1.3 B), and negative correlations with abundance (Figure 1.3 C) and range distribution changes (Figure 1.3 D). This importance is reemphasized through the t-tests and box plots, specifically for richness (Figure 1.2 B) and abundance (Figure 1.2 C). Outlier studies that observed strong increases in bumble bee abundances and decreases in butterfly richness and abundance provide region-specific and species-specific (rather than taxa-specific) examples where few taxa have benefited from changing climate conditions. Lastly, all response category PCAs indicate that temperature acts as a strong representative variable, which confirms the importance of studying climate change and its impact on species diversity. However, temperature change did not negatively correlate with the "response" metric of any PCA and instead had correlations to other variables such as taxa and region. As a result, this presents the importance of species context, in the form of species diversity and habitat/regional diversity, and how landscape and community resilience may be more revealing of climate change effects on species responses.

5. Discussion

Previous literature that studied the response of bumble bees and butterflies to climate variables emphasized the complexities of species traits, phenology, distribution, and population patterns over time. All publications agree that climate change is happening, but the effect of such change on pollinators is less certain (Dornelas & Daskalova, 2020). As highly mobile species

with the potential to migrate in response to warming temperatures, changing habitats, and floral resource availability, bumble bees and butterflies offer opportunities to ascertain species' responses to unprecedented conditions and use these responses as indicators of ecosystem resilience.

The evidence and agreement statements provide one way in which responses and species nuances can be parsed out in more detail. While evidence was limited for bumble bees, some responses had medium and even high confidence in the limited findings. For butterflies, the evidence was more robust, but this did not necessarily lead to higher confidence in species responses. Both groups show evidence of changing species emergence and phenological cues, as well as evidence of potential phenological mismatch through the desynchrony between plant and pollinator emergence periods. Previously, literature focusing on phenological mismatch prioritized bee taxa (Burkle & Alarcón, 2011), and this study affirms that changes may be more widespread across pollinator groups.

For population dynamics, bumble bees showed low confidence in trends in changing richness (decrease) and abundance (increase), while butterflies have seen decreases in abundance and slight evidence for increases in richness. One proposed driver of pollinator declines that was not highlighted in this study is the increased pervasiveness of non-resident and resilient species, which has shown to strongly impact both pollinator richness, abundance, and health (IPBES, 2016). In this meta-analysis, less than 10 papers examined the effects of non-native species; rather, the focus was centered more so around migratory species that could be negatively impacted by changing climate. The response of invasive species on pollinator persistence varies; species generalists may benefit from the introduction of new alien plant species, while species specialists may lose previous abundant floral resources or be outcompeted for resources due to

the species invasion (Biesmeijer et al., 2006; Ghazoul, 2004; Potts et al., 2010). Butterfly literature reported this response as well: the species specialist data trended towards declining populations, while the species generalist data trended towards increasing populations. These responses, however, were very limited in evidence, and it speaks to the significance of habitat and resource generalists within butterfly communities and how introduced species may shift community dynamics. Generalist, non-native butterflies and bumble bees that can expand their habitat range, utilize different floral resources, and change their behavioral patterns will be more resilient because, genetically and physiologically, they are more capable of adapting to changing conditions (Kitahara & Fujii, 1994). Specialist butterflies or bumble bees, on the other hand, do not have the genetic fitness to outperform amongst generalist species, especially if their favorable floral resource becomes threatened as well or their preferential habitat and environmental conditions become scarce. Behavioral life strategies, such as producing multiple generations during a growing season or overwintering as adults, may have positive effects on generalist species as well (Altermatt, 2010). This explains the outperformance of generalist, non-native species in the age of climate change; landscapes may start to see an overabundance of common, generalist species like the Cabbage White or European Skipper over the once prominent Regal Fritillary or Monarch butterfly. As such, further climate/species studies should differentiate between resident and alien species in more depth to better understand the nuances between life histories, floral resource use and availability, and preferred habitat types of these species' groups.

The PCs for pollinator responses to temperature change highlighted the relationships between temperature and species responses such as emergence, range distribution, richness, and abundance changes. These trends mirror the t-test results that emphasized differences between

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bumble bees and butterflies. The intensity of climate variation, as seen through temperature changes, had strong variable representation and correlation but not necessarily towards the response variables studied within the PCAs. Out of all t-test response categories and PCAs, changes in species richness were among the least significant, which may indicate that temperature has not caused as much variation in species richness as other response variables. Species emergence and range distribution changes were most similar in their responses to species and were more correlated (positively and negatively) to study regions. These results may act as justification for the fact that indirect drivers of climate change, in the form of habitat changes and resource availability, may be more telling about species responses than the direct effect of temperature warming itself. These findings were surprising and argue that climate change, while informative in predicting species responses, requires region- or study-specific understandings for species behavioral responses.

Lastly, the distribution studies presented similar remarks: bumble bees and butterflies, on average, have observed range contractions, with a few exceptions that fall into the non-native or resilient species category. While the cause of these range contractions may be less certain, whether due to direct warming temperatures, changing habitats, or species interactions, this finding is significant and has been translated to species observed worldwide. Landscape connectivity might offer buffers to the species facing range contractions; however, additional sampling and documentation that observes such species' responses, coupled with continued conservation of critical habitats for pollinator diversity, may be the saving grace for these insect taxa.

5.1 Visualizing and summarizing species trends

Figure 1.4 presents these species responses by functional group and in relation to differing climate variables and habitat types; given the availability of species-specific responses as mentioned above, these patterns were generalized in relation to the taxa-wide data available, and with additions from other climate variables such as precipitation changes and extreme weather events. The "benefits" of climate change and extreme climate events were observed in six bumble bee and 44 butterfly studies. In a few instances, warmer temperatures and changing conditions such as a fire occurrence caused increases in species richness and abundance over time. In some instances, species relationship studies indicated earlier phenological (both floral and pollinator) emergences that led to additional species generations within a growing season; however, these patterns had not become desynchronized over time.

15 bumble bee studies and 59 butterfly studies reported detrimental species responses to climate variation. As highlighted through this analysis, many species relationships observed declines in species richness, abundance, or range contractions in response to climate variables, and primarily in response to temperature change. Snowpack changes were more pronounced in their responses towards bumble bee species; earlier snowmelt dates led to earlier phenology (floral) emergence, but not always pollinator emergence. Both bumble bee and butterfly species with localized, specialized relationships tended to decrease in population in response to climate variables than species with wide distributions and generalized plant relationships. For butterflies, univoltine species that favored early spring emergence also declined more consistently than those that could produce multiple generations (multivoltine) throughout the growing season, and this was related to a higher probability of climate extremes observed in the spring. These species responses speak to the resilience, or lack thereof, of pollinator species amidst a changing climate,

and how their genetic, behavioral, and physiological functions may not be capable of adapting under future climate scenarios.

The uncertain population response category yielded results with stronger emphases on land use land cover change. For the butterfly literature specifically, in which more authors called out land use change as a primary determinant in species response trends rather than climate, 61 studies emphasized land use change in conjunction with climate variables, while the other 52 papers did not use this as a study parameter. Out of all the bumble bee literature, only five publications emphasized land use change as a probable cause of species decline. Land use change is classified as shifts in habitat connectivity, degradation or modification, agricultural intensification, abandonment, or urbanization, and this driver has ample literature to argue its impact on pollinator decline (IPBES, 2016; Sánchez-Bayo & Wyckhuys, 2019; McLaughlin et al., 2002; Forister et al., 2010; Erhardt, 1985; Hallmann et al., 2017). These studies argued that floral resource quality and quantity, as well as habitat conservation, would be more critical to maintaining species richness, abundance, emergence, and distributions, regardless of whether climate variables continue to change ecosystems in the future. They also justified increases in populations, either in the form of species richness, abundance, or range distribution, through land use changes that were beneficial to species, and particularly generalist, adaptable populations. All publications identified evidence of "climate change" through warmer temperatures, changes in precipitation cycles, increased prevalence of climate extremes, reduced snowpack, and/or earlier snowmelt dates during the study period. However, across both bumble bees and butterflies, the uncertain changes in species responses were accompanied by very low confidence, and nearly all had limited evidence to make conclusive remarks.

In an additional Web of Science literature search, bumble bees AND land use change*

yielded 85 results, with 50 of these articles being relevant based on filters for search replicates,

followed by article title assessments. Bumble bees AND land cover change* yielded 20 results,

with nine of these articles being relevant based on filters for search replicates, followed by article

title assessments. Butterflies AND land use change* yielded 632 results, with 152 of these

articles being relevant based on filters for search replicates, followed by article title assessments.

Butterflies AND land cover change* yielded 196 results, with 42 of these articles being relevant

based on filters for search replicates, followed by article title assessments. Further analyses that

assess these literature findings may further refine additional articles relevancy for this meta-

analysis that are currently categorized within the "uncertain effect" response groups. However,

this cursory literature search reaffirms that the coupling of land use change with changing

climate variables will increase confidence and evidence in pollinator status and future trends

(IPBES, 2016).
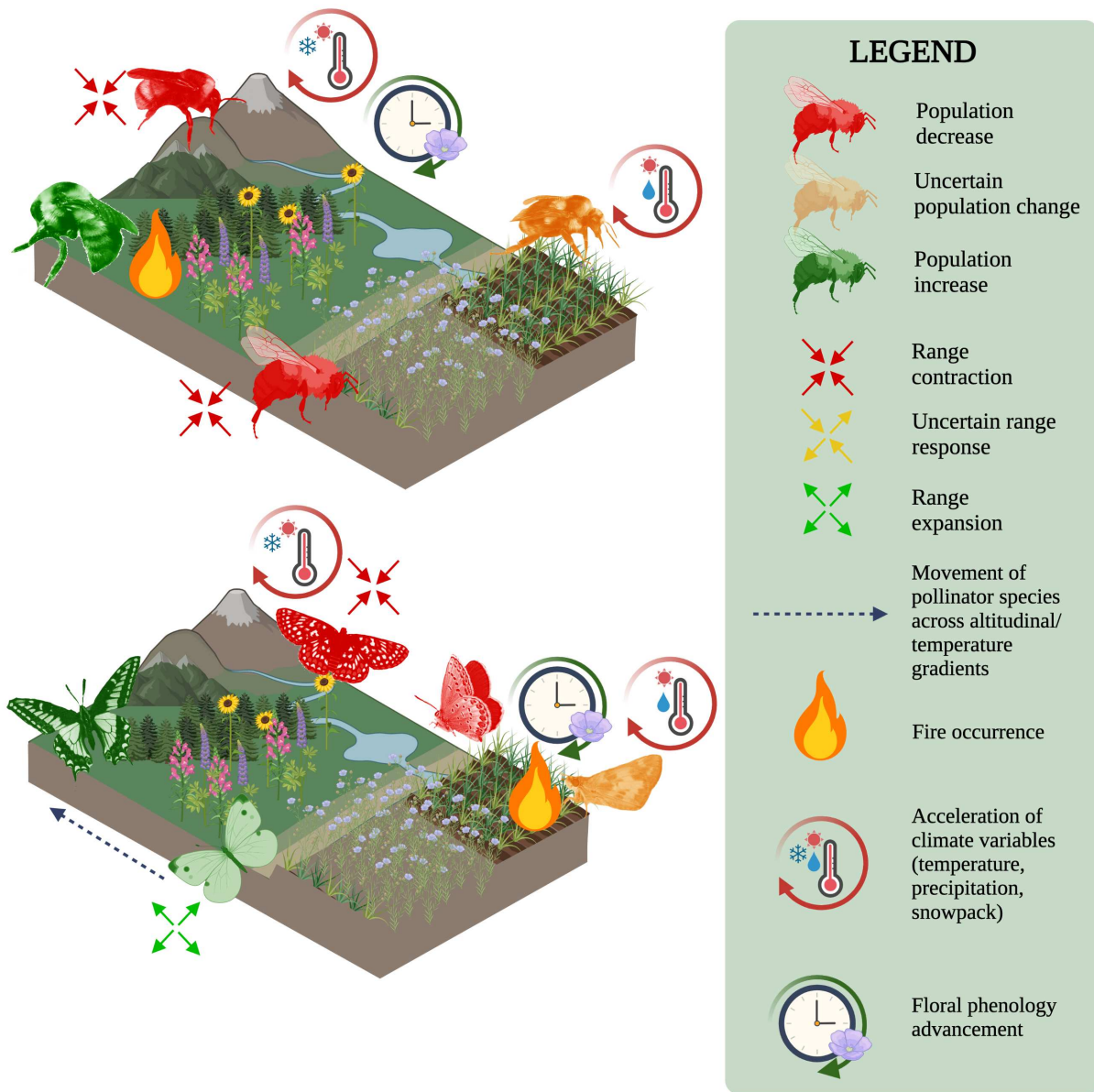
Figure 1.4. Species schematics based on responses to climate variables observed in the literature. The species icons included do not necessarily represent species-specific patterns observed in the literature; rather, this figure serves as the general response of bumble bees and butterflies. Populations of bumble bees and butterflies found at higher altitudes and in areas with climate and land use changes faced greater rates of decline, while species capable of adapting to landscape pressures (i.e., generalists and non-native species) increased in population sizes. Some species had mixed, uncertain responses to climate variables. Figure created with BioRender.com.

6. Conclusion

Pollinators are facing multiple drivers of species decline, including climate change and, in some instances, land use change. While the strength of driving variables is at times uncertain, the trends of earlier species emergence, phenological mismatches, and range contractions are evident depending on the pollinator functional group of concern. Bumble bees and butterflies may respond to these pressures in similar ways at times, but the nuanced effects on species traits and plant-pollinator relationships vary, and therefore, the solutions are complex in nature. Researchers continue to search for clear, effective solutions to mitigate the effects of the above-mentioned threats, but habitat preservation and species monitoring will be the most important responses to prevent greater issues of species decline. This will guarantee that pollinator services can still be used to their fullest extent, thereby ensuring stable food systems and ecosystem resilience for the foreseeable future (IPBES, 2016). These findings should be used, not to fear the inevitable fate of pollinator decline, but rather to prioritize species monitoring amongst locations with historic data availability and an understanding of behavioral responses that may better inform the direct and indirect causes of species changing based on climate change over time.

CHAPTER 3, STUDY 2: POLLINATOR COLLECTIONS WITHIN THE GREATER YELLOWSTONE ECOSYSTEM: TRENDS, PATTERNS, AND ADDRESSING SYSTEMATIC BIASES WITHIN VIRTUAL DATABASES[1]

1. Summary

Biodiversity loss amplifies the need for taxonomic understanding at global, regional, and local scales. Pollinators (bees and butterflies) are two functional groups with public attention for protection, yet little long-term data availability. National Parks, including those in the United States, act as optimal sites to study biodiversity loss, but historic data tends to vary in availability. This study addresses systematic taxonomic and digitization biases present within historic (museum), modern (citizen science), and non-digitized (private collection) datasets for Yellowstone and Grand Teton National Parks from 1900-2021. We find that, although database record availability is representative of butterfly and bumble bee groups known for the area, categories such as data rescue, digitization/availability, and management/archiving vary across database types. These findings offer opportunities for conservationists to understand the efficacy of virtual datasets in addressing questions of species loss over time, including the strengths and pitfalls of digitized data collection efforts.

2. Introduction

Natural history collections (NHCs) have rich histories worldwide and act as repositories for specimens of all kinds, from rare and endemic species of flowers to pests and invasive insects. However, the potential of NHCs to explore landscape changes based on species collections is largely overlooked (Meineke et al., 2019). NHCs have been used to highlight the impacts of climate change on biodiversity, especially for insects and plants, but these efforts have often

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[1]Submitted as Whipple, S., Bowser, G., & Halliwell, P. (2023). Pollinator collections within the Greater Yellowstone Ecosystem: trends, patterns, and addressing systematic biases within virtual databases. *BioScience*.

been restricted to a few specimens, small regions, and short time periods (Kharouba et al., 2019). Researchers have yet to connect biodiversity interactions over time back to species' phenological changes, and NHCs provide opportunities to execute such connections (Polgar et al., 2013). The historical reference of pollinators (bees and butterflies) is of particular concern as species decline occurs nationally and internationally (IPBES, 2016)—because of this, there is an "urgency" to document species diversity through NHCs and other data repositories (Cobb et al., 2019).

NHC digitization efforts are being accelerated through several initiatives to integrate biological collections into education and research projects (Biodiversity Collection Network, 2019) with available taxonomic and genetic information. SCAN (Symbiota Collection of Arthropod Network) acts as the primary NHC digitization repository for North American arthropod collections (185 collections in total), with other large-scale biodiversity collection tools such as the GBIF (Global Biodiversity Information Facility) and iDigBio acting as larger repositories for all taxa within NHC digitization discussions (Cobb et al., 2019). In an initial synthesis of North American collections, Cobb et al. (2019) found that ~95% of North American insect specimen labels have yet to be transcribed for research purposes, and about two percent of specimens have been digitized with images (see Appendix B2 for digitization statistics relevant to this study). With National Science Foundation NHC target digitization trajectories, the group projects that 38% of all current North American arthropod specimens can be digitized by 2050, and less than one percent of collections will be digitized with images. As NHC records become available to the public through the digitization of specimens, these data will become useful in conjunction with citizen science and other recent biodiversity collection projects (Meineke et al., 2019, Kharouba et al., 2019). However, digitization capabilities vary across collections, with percentages of complete databases tied to the size of the collection, resources available, and

funding tied to taxa-specific questions (Cobb et al., 2019). With the addition of citizen science data repositories that act as recent collection tools, researchers can assess species occurrences and upload observations more rapidly than the digitization process allows for, and this can help in the understanding of species changes over time.

When connected with multiple records, species groups, and field sampling protocols, NHC studies have successfully tracked progressions in insect flight periods, temperature responses, genetic variation, and voltinism stages that are all tied to warmer temperatures and other climatic pressures, but these efforts have not happened within the Rocky Mountain region, or more specifically, the GYE (Greater Yellowstone Ecosystem) (Brooks et al., 2014; Kharouba et al., 2019). Both parks have historical records in federal, academic, and local museums, as well as private collections, but there are less known collection efforts in the neighboring national forests and private lands within the GYE and no synthesis of all available historical records in virtual databases. While these datasets provide an understanding of historical species presence, the crosswalking of datasets to assess species occurrence patterns has not happened, and this is a common problem observed across biodiversity studies intending to utilize digitized records (Hardisty et al., 2022).

For this study, "collections" are defined as those that are publicly available through online databases. This includes resources coming from large biodiversity repositories, such as iDigBio, GBIF, and SCAN, smaller biodiversity repositories, such as individual university databases, citizen science databases such as iNaturalist, and a review of the National Park Service (NPS) research permitting reports relevant to bumble bees and butterflies. When a non-digitized dataset was known, such as a private collection or a count list, these resources were also included. Because of the uncertainty in digitized records compared to all available records, this

study holds the caveat that species occurrence patterns for the area may change with greater digitization efforts and collection availability over time. The addition of citizen science records as well as permit-reported data acts as an effort to account for digitized data uncertainties. This effort also aims to rank the status of species diversity records within the known databases in their ability to answer questions surrounding data rescue, digitization/availability, and archiving/management, which translates beyond the GYE to larger questions surrounding biodiversity loss and systematic digitization priorities. Data rescue is defined as the preservation of datasets, whether digitized or not, for scientific use. Data rescue includes the completeness of data, such as the preservation of temporal, spatial, and species-level identification data. Digitization/availability are defined as the percentage of records stored online and the ease with which the data is accessible for the public to use. Last, the archiving/management of records is defined as the continuation of updating taxonomic understanding as well as the reporting of collection and digitization efforts.

2.1. Study goals

This study provides an overview of available pollinator (bumble bees and butterflies) data for the GYE to inform researchers on previous collection priorities, and to present an overview of the status of known species diversity that can inform conservation strategies. Broadly, pollinator data for groups such as bees and butterflies is more available in collections because of their charismatic species groups (Cobb et al., 2019) and benefits to ecosystem services (IPBES, 2016). However, taxonomic and database digitization biases present within current datasets are uncertain, and therefore, data for certain species within these groups may be limited. Before addressing questions such as species range shifts or pollinator declines, baseline data

understanding is needed that can act as evidence for any species changes that have occurred. This is especially important as ecosystems face panarchy, or irreversible rates of change, and species will need to become more resilient towards shifting landscapes or risk rapid rates of decline (Holling, 1973; Gunderson & Holling, 2002; Winfree, 2013; Bodin & Wiman, 2004; Gunderson, 2000). NHCs and other virtual datasets, as a result, may act as critical time capsules for biodiversity by documenting resilient and non-resilient species in perpetuity.

The following questions guided this research: what pollinator species (bumble bees and butterflies) were known or documented to occur within the GYE from 1900-2021, and what patterns are observed within virtual databases regarding digitization and species understanding efforts? I hypothesize that the current knowledge of pollinators is biased towards certain taxonomic groups, leading to gaps in species understanding and potential underestimations of the importance and conservation needs of other pollinator groups. Taxa that are more charismatic and showier, such as the Nymphalidae butterflies and bumble bees, will be more prominent in the databases than lesser-known and smaller taxa, such as the Hesperiidae butterflies. Baseline species understanding for other pollinator groups, such as other bee species and flies, will not be feasible as previous research prioritized charismatic taxa over lesser-known groups of insects. Similarly, databases will be biased in the data reported and available for varying taxonomic groups, even among the bumble bee and butterfly groups. These data digitization biases will reflect not only the collector histories stored within the NHCs but also the resources, personnel, and taxonomic specialties of the subsequent collections. Taxonomic and database digitization biases, therefore, may significantly influence one's ability to inform overarching questions such as biodiversity loss for broad groups such as pollinator species.

3. Methods

3.1 Dataset preparation

All digitized NHC and citizen science records available for the counties within Yellowstone (YELL) and Grand Teton (GRTE) National Parks and surrounding areas from 1900-2021 were tracked for two functional groups of pollinators: butterflies (order Lepidoptera) and bumble bees (order Hymenoptera, family Apidae, genus *Bombus*). Online species NHC downloads were filtered first by location, a 60-kilometer bounding box containing the two parks and surrounding GYE area, then by the respective taxonomic level. Within butterflies, species were filtered based on the five butterfly families observed within the park: Hesperiidae (Skippers), Lycaenidae (Blues and Hairstreaks), Nymphalidae (Brush-footed Butterflies), Papilionidae (Swallowtails), and Pieridae (Whites, Sulphurs, and Yellows). Datasets with relevant, digitized records included: GBIF (GBIF, 2022a, 2002b, 2002c, 2002d, 2002e, 2002f), SCAN, the Smithsonian Institution, *Bombus* of Canada, the Lepidopterist's Society, iDigBio, BugGuide, and iNaturalist. These databases were selected as primary online resources given their frequency of use within the NHC and entomology literature (Cobb et al., 2019). For a full list of repositories housed within databases such as GBIF, SCAN, and iDigBio, including federal, state, and university repositories, see Appendices B1 and B2.

Datasets with known relevant, nondigitized records included: Yellowstone's Fourth of July Butterfly Count records (Marilyn Lutz, NPS, Joshua Tree, CA, personal communications, September 30, 2018), the Yellowstone Heritage and Research Center, and the Harp Collections (Chuck Harp, Colorado State University, Fort Collins, CO, personal communications, January 20, 2019). To account for gaps in species data that have yet to be digitized but may be stored within NHCs or private collections, the NPS research permit and reporting system database was

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searched for both GRTE and YELL by reviewing research investigator annual reports (IAR) publicly reported since 1991 with ties to pollinator, bumble bee, and butterfly research. The IAR system within the NPS requires data reporting prior to permit resubmission, so this database can provide baseline data from each approved research project done in the park, even if a project did not collect specimens or have the resources to digitize their specimen collections. The database was searched by each park with the key terms "pollinator(s)," "bees," "*Bombus,*" "butterfly(s)," and the five butterfly families individually; this ensured all relevant permits were viewed. Data that included species-level identifications and specimen counts were added to the list of available historic records.

When available, data from online repositories were queried using the DarwinCore format, a biodiversity archive standard that includes taxon, occurrence, and event metadata (Wieczorek et al., 2012). This ensured that duplicates present within overlapping databases, specifically within data repositories such as GBIF, iDigBio, and SCAN, could be filtered out of the final analysis. All data were prepped using the "tidyverse" package in R (Wickham et al., 2019). Databases were cleaned based on their robustness of records; first, by the number of total occurrences and its proportion of digitized (i.e., records with complete metadata, including images) records, as well as records with complete taxonomic, georeferenced, and temporal information. Records that were incomplete were flagged but not omitted from the final analysis. All data, including the analysis, are available for download and use on GitHub (Whipple, 2022).

3.2 Virtual database robustness analysis

I followed a three-step analysis of available data to ensure that comparisons between species diversity and database completeness could effectively occur given the availability of the

data. First, I evaluated the online databases (including the NPS research permits) and in-person collections for data quality and quantity. To answer this question, I ran a χ^2 test in Microsoft Excel to compare the relationship between butterfly species families and genus *Bombus* observations within the databases (n=47 databases). P-values less than 0.05 indicated that database records were significant in comparison to expected species occurrences.

3.3 Species diversity data analysis

Next, I calculated species richness and evenness indices across both parks, outside of the parks, and in the overall area using all online, in-person, and research permit records with species-level identifications. For this, the Shannon-Wiener Index (*H'*), Pielou evenness (*J*), and Shannon-Wiener Effective Diversity Number ($e^{H'}$) indices were used (Hill, 1973; Smith & Wilson, 1996). All calculations were performed using the "vegan" package in R (Oksanen et al., 2013). Higher Shannon-Wiener Index values represent more diverse areas of species diversity; these values typically fall within the range of 1.5-3.5. Pielou evenness values closer to one indicate a richer, more evenly dispersed species diversity seen across the area.

3.4 Species data gaps analysis

Finally, given gaps in data availability within online databases due to the digitization process, I ranked all occurrence data in relation to categories of data rescue, digitization/availability, and archiving/management. Each database category (federal, citizen science, state, private, mixed-source, and university records) was scored using a Spearman rank correlation method in Microsoft Excel based on digitization metrics. Digitization metrics relied on database reporting available online and followed a 0-100 scale for the data rescue, digitization/availability, and archiving/management categories. A Spearman rank correlation

coefficient less than the critical value for n=6 indicated a significant correlation between categories and databases.

4. Results

For an overview understanding of available records by database type and taxonomic group, as well as a database overview and digitization statistics, see Appendices B1 and B2. There were only five records for the Rionidae family (Metalmarks), so this butterfly family was omitted from analysis. The following records could be refined based on currently known ranges: *Bombus lapponincus*, four records; *B. terricola*, one record; and *B. vosnesenskii*, two records. For butterflies, the following species only had one observation within the databases, or species identifications could be refined based on currently known ranges: (*Anthocharis cethura, Euchloe lotta, Pieris oleracea, Pieris virginiensis, Papilio canadensis, Oeneis alberta, Oeneis macounii, Euphilotes glaucon, Cupido comyntas, Satyrium acadica, Erynnis pacuvius lilius, Hesperia leonardus, Hesperia ottoe, Hesperopsis alpheus, Megathymus streckeri, Oarisma edwardsii, Hesperopsis libya, Polites rhesus, Polites vibex,* and *Pompeius verna*). Six records were only identified at the family level (four Lycaenidae and two Pieridae), and three records within the Nymphalidae were only identified at the subfamily level (Limenitidinae). Within *Bombus*, 39 records from online databases were only identified down to the genus level, and 213 records had no locational or temporal information available.

To address database robustness in species diversity understanding, χ^2 values less than 0.05 at the 95% confidence interval indicated there was a statistically significant relationship between species observed across databases. χ^2 results show that the genus *Bombus* and all butterfly families have significant database representation for the observed species occurrences compared to the expected values ($p < 0.05$) (Table 2.1). This provided baseline evidence of the

database's completeness that could inform subsequent patterns of species richness and evenness within known, digitized historic, and citizen science records. This step was critical given the uncertainties in data availability based on variations in digitization efforts across repositories.

Table 2.1. χ^2 values for each taxonomic group observed across the databases with GYE records (n=47), and p-values to represent database significance in representing expected species. P-values less than 0.05 are denoted with an asterisk (*), meaning that the observed database representation is significant and representative of the population compared to the expected values.

	Bombus	Hesperiidae	Lycaenidae	Nymphalidae	Papilionidae	Pieridae
χ^2	5022.05	1985.43	1283.85	2405.66	1086.32	435.22
p-value	0*	0*	8.82×10^{-239}*	0*	1.76×10^{-197}*	8.27×10^{-65}*

Collection years varied across *Bombus* and the five butterfly families from 1900-2021 with no "peak" sampling year consistent across groups. Since 1991, GRTE and YELL have approved 116 research permits related to pollinator work, many of which resulted in repeat sampling efforts (24 unique research permits total). An additional, unknown number of specimens were included within the research permits for *Bombus sp.* and butterfly species of all five families. Figure 2.1 outlines the total collections available for each taxonomic group by location (n=10,051 records). For a breakdown of the most common species collected, see Figure 2.2.

Available Pollinator Species Records by Location
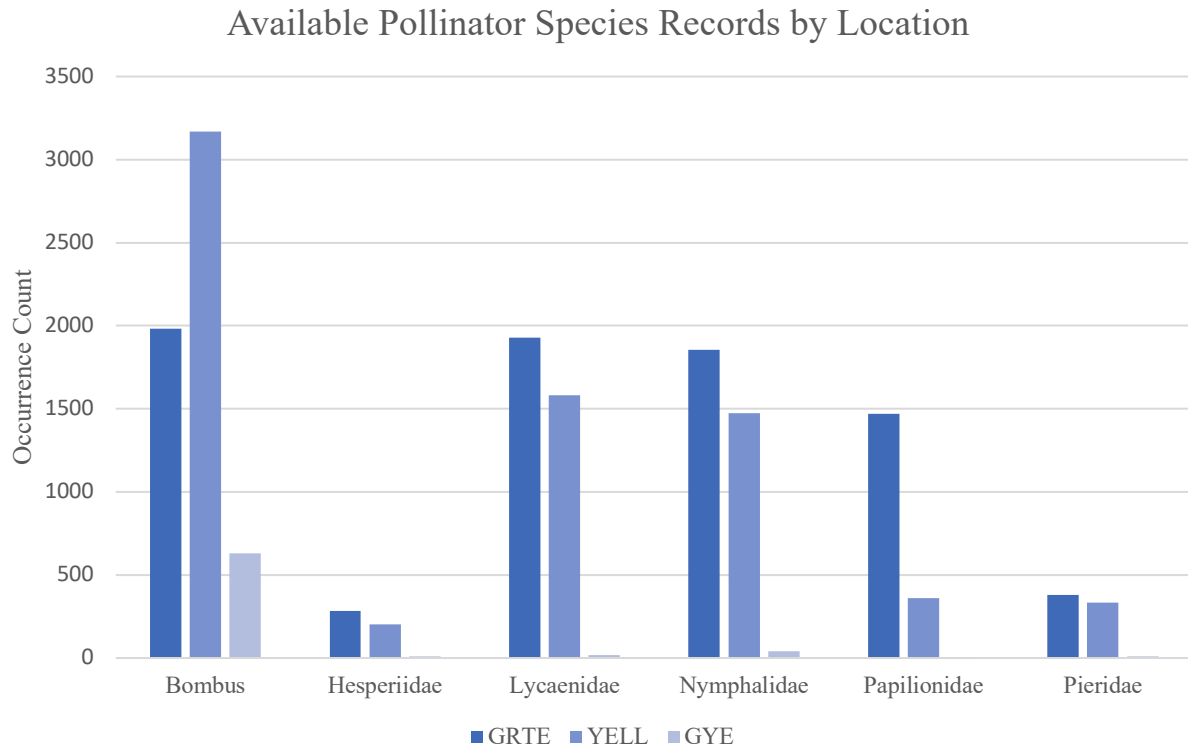
Figure 2.1. Pollinator species records by location (GRTE, YELL, and outside of the parks (GYE)). The total records across all five butterfly families and genus *Bombus* is 10,051.
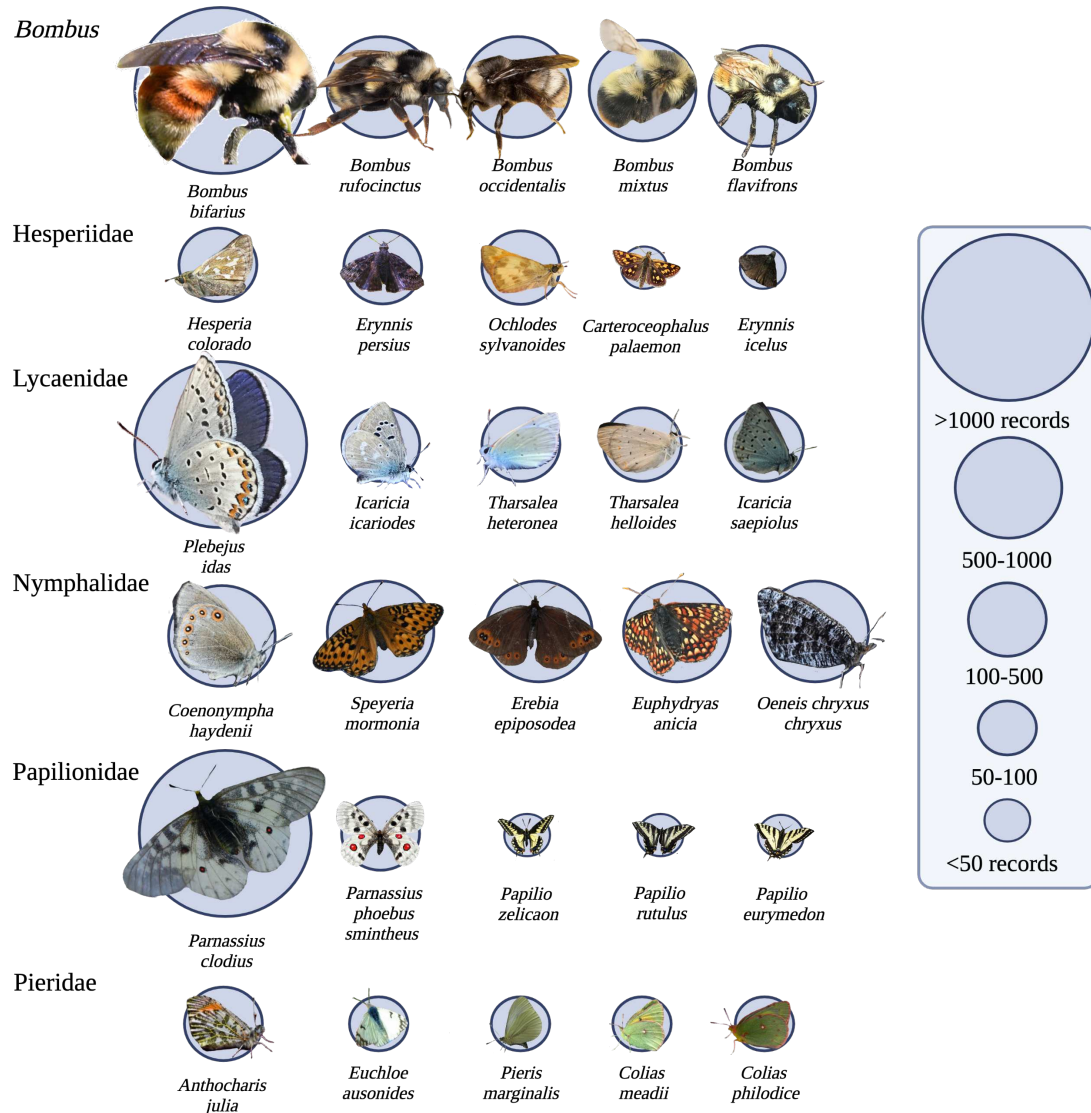
Figure 2.2. Species breakdown of most common occurrences by taxonomic group. For genus *Bombus*, *B. bifarius* = 1643 records, *B. rufocinctus* = 902 records, *B. occidentalis* = 765 records, *B. mixtus* = 560 records, and *B. flavifrons* = 537 records. For family Hesperiidae, *Hesperia colorado* = 105 records, *Erynnis persius* = 57 records, *Ochlodes sylvanoides* = 54 records, *Carterocephalus palaemon* = 42 records, and *Erynnis icelus* = 29 records. For family Lycaenidae, *Plebejus idas* = 1820 records, *Icaricia icariodes* = 259 records, *Tharsalea heteronea* = 198 records, *Tharsalea helloides* = 137 records, and *Icaricia saepiolus* = 127 records. For family Nymphalidae, *Ceoenonymha haydenii* = 418 records, *Speyeria mormonia* = 363 records, *Erebia epiposodea* = 183 records, *Euphydryas anicia* = 181 records, and *Oeneis chryxus chryxus* = 180 records. For family Papilionidae, *Parnassius clodius* = 1299 records, *Parnassius phoebus smintheus* = 427 records, *Papilio zelicaon* = 51 records, *Papilio rutulus* = 23 records, and *Paplilio eurymedon* = 18 records. For family Pieridae, *Anthocharis julia* = 118 records, *Euchloe ausonides* = 88 records, *Pieris marginalis* = 76 records, *Colias meadii* = 72 records, and *Colias philodice* = 70 records. All photograph credits of S. Whipple, G. Bowser, and additional field interns.

Shannon-Wiener Index, Pielou evenness, and effective (true) Shannon-Wiener Index diversity values were calculated across taxonomic groups, and with consistencies in rankings amongst regions and families (Table 2.2). Because of the diversity and sampling uncertainties presented within the Shannon-Wiener and Pielou evenness indices, the Shannon-Wiener Effective Diversity Number provided an equivalent, hypothetical understanding of species diversity to the observed ecosystem. I did this to minimize sampling biases seen across taxa, areas, and years within the species occurrence dataset, something that is criticized within richness and evenness studies that utilize these analyses for biodiversity understanding (Strong, 2016). Like the Shannon-Wiener Index, higher values represent true, diverse equivalent areas of species diversity that are minimized by sampling biases.

In GRTE, YELL, outside of the parks, and within the GYE overall, family Nymphalidae had the highest Shannon-Wiener and Effective Shannon-Wiener Index, while family Papilionidae had the lowest values across all locations except for outside of the parks, which had the lowest value for genus *Bombus*. For Pielou evenness, family Pieridae had the highest value in GRTE, YELL, and across the overall area. Family Hesperiidae had the highest evenness value for the outside of the park records. In contrast, the genus *Bombus* had the lowest evenness value outside of park sampling areas, the Papilionidae had the lowest value in GRTE and YELL, and the Lycaenidae had the lowest overall value. More variation occurred across families for middle ranking richness and evenness values. There were minimal historic or citizen science records available for Papilionidae outside of the parks (five records), which caused these values to be omitted from the species richness and evenness rankings.

Table 2.2. Shannon-Wiener Index (*H'*), Pielou evenness (*J*), and effective (true) Shannon-Wiener Index diversity (e$^{H'}$) values for specimens across families collected in GRTE, YELL, outside of the parks, and GYE-wide. Shannon-Wiener values that are larger represent more diverse areas based on species diversity. Pielou evenness values that are closer to one represent more evenly diverse areas based on species diversity. Asterisks are used to represent highest values (***) compared to lowest values (*) across taxonomic groups and areas. (#) indicates presence of no historic or citizen science records for the area.

	Bombus	Hesperiidae	Lycaenidae	Nymphalidae	Papilionidae	Pieridae
Shannon-Wiener Index (*H'*)						
GRTE *H'*	2.14	2.33	2.26	3.34***	0.59*	2.30
YELL *H'*	2.35	2.77	1.79	3.25***	0.59*	2.47
Outside of Parks *H'*	1.66*	1.70	2.29	2.92***	0#	1.91
GYE *H'*	2.29	2.65	2.09	3.38***	0.83*	2.49
Effective Shannon-Wiener Index diversity (e$^{H'}$)						
GRTE e$^{H'}$	8.53	10.24	9.55	28.21***	1.80*	10.00
YELL e$^{H'}$	10.51	15.94	5.97	25.70***	1.80*	11.84
Outside of Parks e$^{H'}$	5.27*	5.45	9.91	18.53***	1#	6.72
GYE e$^{H'}$	9.87	14.11	8.12	29.33***	2.30*	12.02
Pielou evenness (*J*)						
GRTE *J*	0.26	0.31	0.22	0.24	0.13*	0.32***
YELL *J*	0.28	0.30	0.19	0.24	0.13*	0.32***
Outside of Parks *J*	0.25*	0.45***	0.37	0.30	NA	0.43
GYE *J*	0.27	0.30	0.20*	0.24	0.20	0.31***

The Spearman rank correlation results indicate that the relationship between data rescue and archiving/management, as well as digitization/availability and archiving/management was significant across the database categories (above the Spearman rank critical value for 0.05 significance) whereas the relationship between data rescue and digitization/availability was not significant (below the Spearman rank critical value) (Table 2.3). When ranking across the three

categories, database categories such as citizen science repositories scored highly in their data rescue, digitization efforts, and management. Out of all categories, private, non-digitized resources scored the lowest in their rankings across all three categories.

Table 2.3. Database category rankings for the three database review categories: data rescue, digitization/availability, and archiving/management. Initial rankings followed a 0-100 scale and were generated based on digitization statistics available online. Critical values higher than 0.829 at the 95% significance level indicated a correlation between categories.

	Rank Correlation		
	Data Rescue	**Digitization/Availability**	**Archiving/Management**
Citizen Science	95	100	75
Federal	75	5	50
Mixed	75	85	75
Private resources	5	0	0
State repository	25	25	25
University	50	25	50
	Data rescue rank	**Digitization rank**	**Archiving rank**
Citizen Science	1	1	1.5
Federal	2.5	5	3.5
Mixed	2.5	2	1.5
Private resources	6	6	6
State repository	5	3.5	5
University	4	3.5	3.5
	Data Rescue + Digitization	Data Rescue + Archiving	Digitization + Archiving
Spearman correlation	0.735294118	0.925476223	0.85084104
N=6			
Critical value for p-value <0.05	0.829		
	Not significant	Significant**	Significant**

5. Discussion

The data indicate that previous pollinator sampling efforts within the GYE varied across taxa, collections, and regions. This analysis did not uncover any missing or expected species from the databases. Rather, it highlighted where there are important shifts in what we know about the species of the GYE and where there are gaps in our knowledge of biodiversity. The Shannon-Wiener Index, Pielou evenness, and effective Shannon-Wiener Index diversity indices emphasize the Nymphalidae species richness seen within the GYE and on a global scale (Freitas & Browns, 2004) (Table 2.2). While family Papilionidae is not the richest or even in species diversity in the GYE, these trends correlate to this group having the fewest number of species within a butterfly family observed in the GYE (Munroe, 1960) and to the previous researchers who had taxonomic biases towards the *Parnassius* butterflies in GRTE and not necessarily within YELL (Figure 2.2) (Auckland et al., 2004, Caruthers & Debinski, 2006). For Pieridae historic records, most were found in and surrounding YELL and GRTE, so the evenness skew seen for this family may be due to the data digitized within current repositories that depict the expected butterfly family's diversity compared to other butterfly groups. Outside of the parks, private collectors with interests in the family Hesperiidae led to higher observations of this group and the species diversity present (rather than a taxonomic focus on a particular species), and this caused the higher species evenness value observed (Chuck Harp, Colorado State University, Fort Collins, CO, personal communications, January 20, 2019). Lastly, *Bombus* richness and evenness values align with the taxonomic structure of the order Hymenoptera, family Apidae (Hines, 2008); for the GYE, there are other groups within Apidae that are more robust in species diversity but lack digitized record availability. As the digitization of more repositories occurs, these values of richness and evenness will change to be more consistent with the weight of insect

species groups across broader taxonomic scales. These taxonomic biases, as predicted, align with the assumption that collection biases occur towards charismatic, well-known species rather than rare, small, or lesser-known taxa.

However, as the digitization of NHCs evolves over time, these metrics will certainly change, as will the systematic taxonomic biases observed across locations (Figure 2.1) and functional groups (Figure 2.2) (Cobb et al., 2019). There are species for which the understanding of its range has changed, or additional time could be devoted to improving a collection's taxonomic understanding. The research permitting review identified 24 unique projects and 116 permits in total, many of which captured specimens from the park for identification or genetic analysis purposes. Researchers with these permits varied from those with taxonomic specializations to those asking climate-phenology questions, those with interests in educational and citizen science opportunities, and those intending to answer genomic questions for rare, endemic, and hybridized species of the area. These efforts provide targeted understanding of certain species but leave data gaps in the status of curation needs; this is a common problem seen in entomological studies, where taxonomic expertise requirements for specimen collections lead to delays in data processing (Kim & Byrne, 2006).

Additionally, the Spearman rank correlation that quantified the status of data rescue, digitization, and database management across the database categories offers an overview of where systematic biases occur. The relationship between data rescue and archiving/management, as well as between digitization/availability and archiving/management, offers opportunities for the prioritization of uploading specimens when possible while also maintaining databases over time (Shirey, 2018; Shirey et al., 2021). These rankings also speak to the importance of database management over time; while collecting and digitizing specimens in the first place is critical to

answering questions about biodiversity loss, the maintenance of species records will be critical as taxonomic understanding and species range distributions may shift over time. Despite the tremendous history of biodiversity and taxonomic work nationwide, researchers recognize that a baseline understanding of species diversity is still lacking (Kass et al., 2022). Nevertheless, the continuation of digitized, online platforms such as NHC repositories, in addition to citizen science platforms, can hopefully mitigate some of these taxonomic bottlenecks in future research endeavors. As found through this study, even charismatic taxonomic groups like bumble bees and butterflies require additional data improvements if collections intend to act as time capsules for future species diversity assessments.

6. Conclusion

The available data for bumble bee and butterfly species in the GYE varied in their range and were spread across federal, university, and local collections with different digitization statuses and taxonomic interests. NHC and citizen science databases will continually evolve as more digitization efforts occur, and this presents ample opportunity for future understanding of species statuses to reflect occurrence availability. Since protected areas are proposed to act as climate refugia for sensitive species diversity given the presumed lower impact of other anthropogenic pressures such as urbanization and habitat degradation (Morelli et al., 2016; Barrows et al., 2020), this study aimed to determine patterns in bumble bee and butterfly data that have previously been collected, and where there are current taxonomic gaps. This effort's findings can inform not only species conservation priorities but also provide evidence of pollinator species status that could be complimented with other datasets, such as climate and phenology data. As concerns over biodiversity loss amplify, researchers need to know how tools

such as virtual NHC repositories and citizen science data can be informative for species monitoring over time. Targets relevant to biodiversity protection cannot be achieved without a prior understanding of the historic and current data availability and species occurrence status in the complex and varying databases. Therefore, more efforts to prioritize data transparency to minimize systematic data biases are needed, especially for priority taxa such as pollinators.

CHAPTER 4, STUDY 3: POLLINATORS IN PROTECTED AREAS: CLIMATE, PHENOLOGY, AND SPECIES PATTERNS OF BUMBLE BEES AND BUTTERFLIES IN THE GREATER YELLOWSTONE ECOSYSTEM

1. Summary

There is robust evidence that climate change has negatively impacted biodiversity worldwide. While the effects of climate change are strongly correlated with patterns such as earlier phenological emergence, little is known about the direct and indirect effects of climate variation on floral resource availability and pollinators (bumble bees and butterflies). Specifically, these relationships are understudied within national parks, which may buffer species from other human-caused drivers of decline. Here, we studied the effect of climate change on floral phenology and pollinator occurrence in Yellowstone and Grand Teton National Parks using virtual, satellite, and field observations. While floral emergence has slightly shifted in the parks by three days since 1980, the effect of this shift on pollinator occurrence is less certain, with the early and late-emerging floral resources having a stronger influence on species occurrence over time. For both floral and pollinator data, the effect of climate had mixed responses—temporal variation had the strongest effect on species occurrence rates over any climate variable measured. These findings offer comparisons for researchers interested in multi-faceted, applied approaches to broad questions such as pollinator decline and phenological mismatch in relation to protected areas.

2. Introduction

2.1 Climate change, phenology, and pollinators

Pollinators—bees, butterflies, beetles, flies, and moths — are a critical component of global food systems and wild plant diversity persistence (Potts et al., 2010; IPBES, 2016).

However, pollinators face multiple drivers leading to population declines, such as habitat loss, fragmentation, non-native species introductions, disease, urbanization, climate change, and more. In the age of climate change, systematic sampling mechanisms of pollinators and plants—both within developed and protected areas—need to occur to track potential drivers of population decline over time, especially with species such as pollinators that are critically dependent on climate and floral resources for survival (Hill et al., 2002). Climate is becoming more variable on a global scale, and these shifts in temperature, precipitation, and other natural hazards over time will have large implications for species ranges and their ability to survive (Svenning & Condit, 2008; Pörtner et al., 2019). Native pollinator species diversity is critical for overall ecosystem functioning, but the current global rate of pollinator species extinction is at least ten times greater than the average rate over the past 10 million years, and these values will continue to accelerate as the effects of climate change worsen (Brondizio et al., 2019).

Pollinators and plants depend on warmer temperatures and sufficient precipitation for emergence, so climate shifts may encourage desynchrony in behaviors; however, little evidence of this relationship has occurred (Burkle & Alarcón, 2011). Historically documented plant-pollinator phenological mismatches have been correlated with rising global temperatures, but these studies have been isolated in nature (Bartomeus et al., 2011). Other studies have tracked the evolution of bumble bee species and tongue length as a response to phenological differences, but the evolution of other dependent floral resources did not occur at similar rates, nor were these phenomena tracked amongst other species (Miller-Struttmann et al., 2015). Some researchers have shown that warmer temperatures may negatively affect bumble bees during overwintering (Oyen et al., 2016) or foraging periods (Richman et al., 2020; Pashalidou et al., 2020); on the other hand, climate change may increase periods of activity in other bee species (Bergman et al.,

1996). Simulated work by Soroye et al. (2020) indicated temperature and precipitation change

had a strong influence on bumble bee decline in North America and Europe, but they

acknowledged that this did not account for other land use change factors.

For butterflies, this functional group have been negatively impacted by the direct effects of

climate change (Forister et al., 2010), and the result of indirect effects through resource

availability is also known for this functional group (Boggs & Inouye, 2012). Crossley et al.

(2021) found that temperature increase had a strong influence on butterfly decline in North

America, whereas precipitation increase showed to benefit populations over time; however, they

only studied these variables from 1993-2018, a period when national climate trends experienced

more variations than previous time scales. Researchers in Europe found that pollinators tend to

fly six days earlier in the present than they did in the 1960s, and that temperature was the most

significant influence for this shift (Duchenne et al., 2020). However, the researchers were unable

to track the phenology longevity of both plants and pollinators over time, and they have

uncertainty about how seasonality will positively or negatively impact different regions and their

pollinator assemblages.

2.2 Pollinators in alpine areas: climate change and ecosystem resilience

Mountain ecosystems and the species living within them are even more vulnerable to the

effects of climate change due to species' historic reliance on winter precipitation amongst

elevational gradients; the Intergovernmental Panel on Climate Change (IPCC) states that these

changes in climate over time will heavily impact seasonal activities, species abundance and

distribution, ecological disturbances, and overall ecosystem functioning (Pörtner et al., 2019).

Species within high-elevation systems are more vulnerable to climate impacts based on the

fluctuations of climate extremes, their intrinsic sensitivity due to life history characteristics, trophic dynamics, and species interactions; however, little evidence of species' adaptive responses has occurred (Moritz & Agudo, 2013). As the impacts of climate change—warmer temperatures, earlier snowmelt patterns, etc.—continue, this will lead to altered community dynamics, such as earlier plant growth and sexual reproduction within spring-blooming angiosperms and earlier emerging insect species (Price & Waser, 1998; Duchenne et al., 2020). Species and ecosystem resilience may change as landscapes face irreversible tipping points of change; this is especially pertinent with pollinator groups that make primary contributions towards ecosystem services (Holling, 1973; Gunderson & Holling, 2002; Winfree, 2013).

Mountains, however, are also considered resilient, heterogeneous landscapes and may fare better than homogenous, topographically similar landscapes in the age of climate change (Rahbek et al., 2019; Auckland et al., 2004; Inouye, 2019). Species-specific responses will vary based on the differences in landscapes due to resource availability and the effects of climate change on such resources. Mountain ecosystems provide elevational gradients that could allow for species adaptations and greater species and system resilience (IPCC, 2019; Gunderson & Holling, 2002). Researchers have assessed the importance of elevational gradients on small mammal, plant, and butterfly diversity distributions and noted that, in the age of climate change, species that are highly mobile will face shifts in ranges to adapt to climatic variations, whereas sedentary species will be at greater risk for extinction (Boggs & Murphy, 1997; Arroyo et al., 1982; Moritz et al., 2008). Adedoja et al. (2018) stated that the most critical species interactions to study are those within the middle elevational zone given the possible need to migrate upwards in altitude as well as species responses to possible resource competition issues with lower elevational migrants. However, all species risk conflict with the introduction of non-native

species, a lack of resources across any range, and the inability to adapt to change (IPBES, 2016). If species with specific habitat requirements are unable to adapt to changing conditions, communities and landscapes are at risk of collapse (Gunderson & Holling, 2002).

2.3 Pollinators in protected areas: climate change and data opportunities

However, connected, protected areas may provide species some safeguard from rapidly changing conditions, and therefore may aid in maintaining species and landscape resilience over time (Gunderson, 2000). Rapid rates of pollinator insect decline have been documented within European protected areas (Hallmann et al., 2017), but pollinator biodiversity inventories, and therefore understanding of rates of decline within United States national parks, are less available (Shafer, 1999). Shifts in species range on the global scale have been observed and documented using museum and herbarium collections, but the amount of information transcribed to track phenological shifts in specimens, both in the field and within natural history collections (NHCs), is limited within the United States (US) (Polgar et al., 2013; Price & Waser, 1998). Due to the insufficient pollinator datasets available within the US National Park Service (NPS), monitoring projects such as those in the European parks have not occurred.

With stronger technological tools, researchers can bridge topics such as climate change, phenological mismatch, and pollinator decline using dynamic mechanisms such as citizen science applications and virtual datasets and apply similar questions to US national parks. Citizen science, the public participation of scientific research, provides the tools, applications, and resources necessary to measure changes in pollinator occurrence throughout the next century while minimizing resource impact (Bonney et al., 2009). US national parks have supported citizen science sampling efforts such as the Backyard Christmas Bird Count, all-taxa biodiversity

inventories, the National Fourth of July Butterfly Count program, and National Phenology Network's Nature's Notebook floral studies (Swengel, 1990; Bloom et al., 2022). Citizen science projects act as some of the most critical data sources for tracking biodiversity changes within US protected areas (Bonney et al., 2009; Bonney et al., 2014). Pollinator-specific efforts have happened within other national parks (Rochefort & McLaughlin, 2017; Scholtens & Wagner, 2007), through BioBlitzes (Lundmark, 2003), and in coordination with museum collections (Clark & Clark, 1951). Citizen science datasets will continue to become richer in both data quality and quantity for both the parks and researchers as technology improves and public interest in scientific discovery grows (NAS, 2018). While citizen science does present some limitations, such as the types of questions that can be asked by a researcher (Ellwood et al., 2017), the effort (and funding) required to successfully implement community help and long-term engagement (Bonney et al., 2014), data biases, and data accuracy (Lukyaneneko et al., 2016; Aceves-Bueno et al., 2017), these limitations are outweighed by the long-term benefits of such data collection and its ability to provide understanding to current data gaps within the parks.

2.3 Climate change, phenology, and pollinators in the Greater Yellowstone Ecosystem

Two protected areas with historic pollinator datasets but limited connections to climate and phenology data include Grand Teton (GRTE) and Yellowstone (YELL) National Parks; these parks are part of the most continuous temperate zone protected landscape in the US, the Greater Yellowstone Ecosystem (GYE) (Yellowstone National Park, 2022). Climate change impacts on the GYE are evident—weather station records from Yellowstone indicate that two of the warmest, driest seasons on record have happened within the past ten years, and the growing season length, amplitude, and green-up cover have all become earlier in the season since more

accurate, comprehensive satellite imagery of the GYE has occurred (Potter, 2020; Hostetler et al., 2021). The area has projected summer temperatures increasing by 3°C under RCP4.5 (stabilization scenario), and up to 8°C under RCP8.5 (business as usual scenario) by 2100 (Pörtner et al., 2022; Hostetler et al., 2021; Westerling et al., 2011). These values are higher projections than the global RCP mean predictions (1.8°C for RCP4.5 and 3.7°C for RCP8.5) (Pörtner et al., 2022). The area is expected to lose nearly half of its current seasonal snowpack, almost 40% of its June-August runoff, and face an increased transition (10%) of precipitation from snow to rain, all by 2100 (Hostetler et al., 2021). In addition, shifts in habitat and elevational zones, from montane and upper treeline zones to more low-elevation-dominant zones, are projected to occur across the GYE due to these climate shifts (Piekielek et al., 2015). These shifts will impact landscapes and species resiliency, but the severity of such impacts is unknown.

Bowser (1988) found that YELL butterfly species differed in phenology more by year than by site, with species' flight periods occurring at the same time across the park. Butterfly species dominance patterns did not differ, nor did the total seasonal diversity between years. In correlation with floral resources, there were no apparent clusters of species between sites or years, indicating that the patterns of host-plant reliance and species diversity were more randomly present than anticipated or observed in other locations nationwide (Bowser, 1988). Previous pollinator data provides a framework to build upon with today's knowledge of the GYE and the impacts that changing temperature, precipitation, and snowpack have had on other species. Sampling efforts for Bowser (1988) would not start until late June because of the presence of snow; now, similar sites are considered snow-free by early May (Hostetler et al., 2021). A resampling of historic sites is especially critical given natural disaster impacts such as

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the 1988 Yellowstone fires, a major disturbance that researchers argue has led to a shift in fire regimes and plant succession patterns for the area that will only continue to evolve in the age of shifting climates (Hansen & Phillips, 2018; Romme, 1982).

More recently, researchers such as Bloom et al. (2022) found that first flowering time in GRTE has advanced since the 1970s, and this could result in pollinator emergence shifts over time as well; however, these direct relationships have not been studied in the GYE. In contrast, a review of changes in spring onset (both first leaf and bloom index) found that YELL and GRTE faced "no extremes" between historic and current trends (Monahan et al., 2016); this indicates opportunities for additional data analyses to understand patterns of change. The intersection between floral resource and pollinator emergence shifts in the form of phenological mismatch within the GYE, however, has not been observed, especially across elevational gradients within the parks and in relation to the parks' changing climate.

2.4 Study goals

Pollinators act as a good measurement of shifts in community structures because of their host-plant reliance and vulnerability to habitat quality (Erhardt & Thomas, 1991). However, little understanding of climate change, species distribution amongst elevational gradients, and phenological patterns in relation to bumble bee and butterfly species distribution has occurred, especially within the United States, the Rocky Mountain region, and GRTE and YELL National Parks (Rykken et al., 2014). Long-term data on pollinator emergence patterns are critical for determining species shifts, yet such long-term data for small organisms is often missing in protected areas. Because of the ever-changing capabilities of technology, I used a mixture of research approaches, including citizen science records, museum collections, climate, and

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phenology datasets, to detect patterns in phenological, climate, and pollinator emergence over time. Additionally, seasonal floral resource availability may be critical indicators of pollinator shifts and potential desynchrony between early and late season species versus mid-season or multi-voltine (multiple flights throughout the growing season) species. Researchers have noted that phenological mismatches and some insect voltinism periods are shifting because of climate change (Duchenne et al., 2020; Cayton et al., 2015; Altermatt, 2010), but this pattern has not yet been documented in the US or within the GYE area.

The following question guided this research: how have GYE floral resources shifted in phenological timing, if at all, and what is the relationship of both pollinator occurrence and phenological trends to observed temperature and precipitation changes? I hypothesize that warmer temperatures and changing precipitation (i.e., earlier snowmelt timing and precipitation transitions from snow to rain) have altered the timing of flowering and the availability of floral resources, which has caused decreases in pollinator occurrences over time (Figure 3.1). Shifts in climate and floral phenology have had larger, negative effects on pollinator occurrences in sub-alpine habitat zones than in lower elevation areas because of accelerated temperature warming and precipitation shifts. Floral resources that are earlier in emergence and may be past peak bloom/resource availability during pollinator flight periods will have negative consequences on species occurrence patterns. This research can inform researchers and land managers on changing species interactions occurring due to climate change within a landscape safeguarded from other land use pressures, such as habitat fragmentation and agricultural intensification, which are causing rapid rates of pollinator decline worldwide (IPBES, 2016). By understanding the severity of change that temperature and precipitation changes have had on floral phenology

and pollinator occurrences, greater efforts for monitoring less resilient species and landscapes

present within these protected areas can occur.
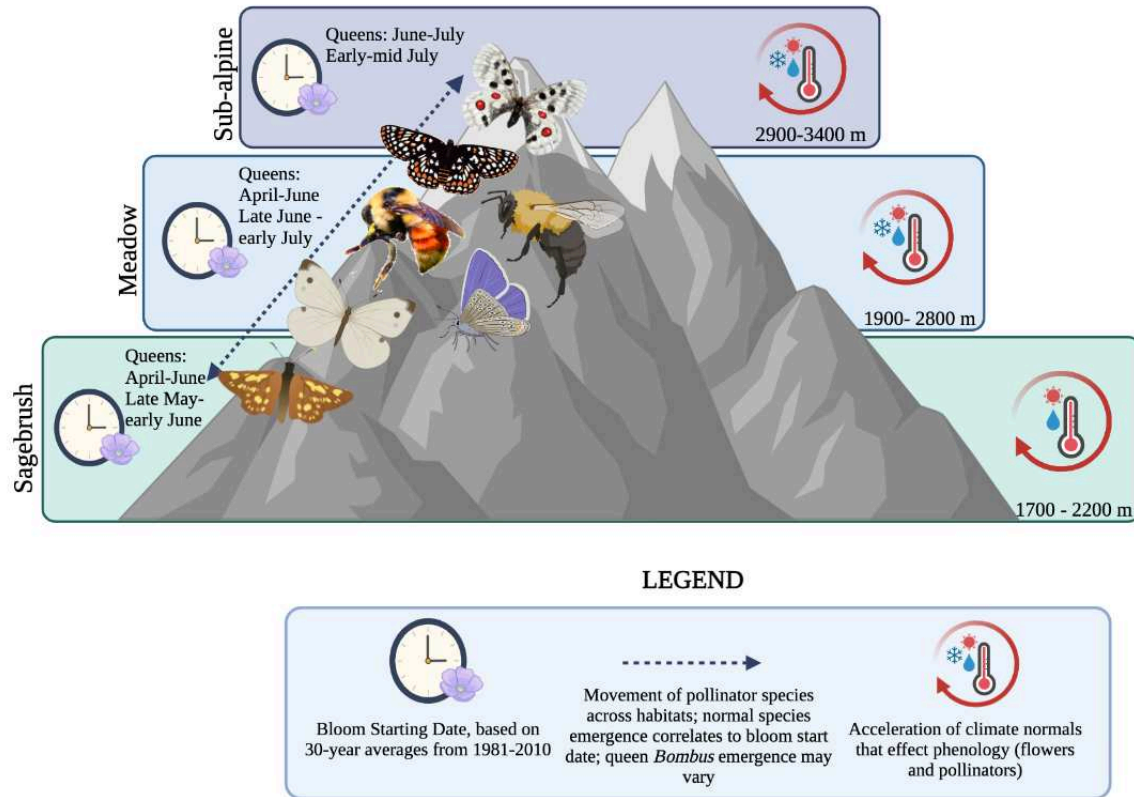
Figure 3.1. Hypothesis of pollinator (bumble bee and butterfly) responses to shifting climate (temperature and precipitation) and phenological timing within the GYE. Timing represents "normal" ranges observed for plant bloom periods across varying habitat types; pollinator emergences are expected to fall within these peak ranges but can extend beyond peak floral periods; and range shifts may occur due to changing climate and phenological timing observed in different habitats. Species emergence along elevational gradients varies across the five butterfly families (Hesperiidae, Pieridae, Lycaenidae, Nymphalidae, and Papilionidae) and the bumble bee genera (genus *Bombus).*

3. Methods

For an overview of data materials, see Figure 3.2. I used various types of data: climate,

floral phenology, and pollinator (bumble bee (genus *Bombus*) and five butterfly families)

occurrences. To have the most robust dataset available for both parks, I relied on additional

sources that will be described in detail below.
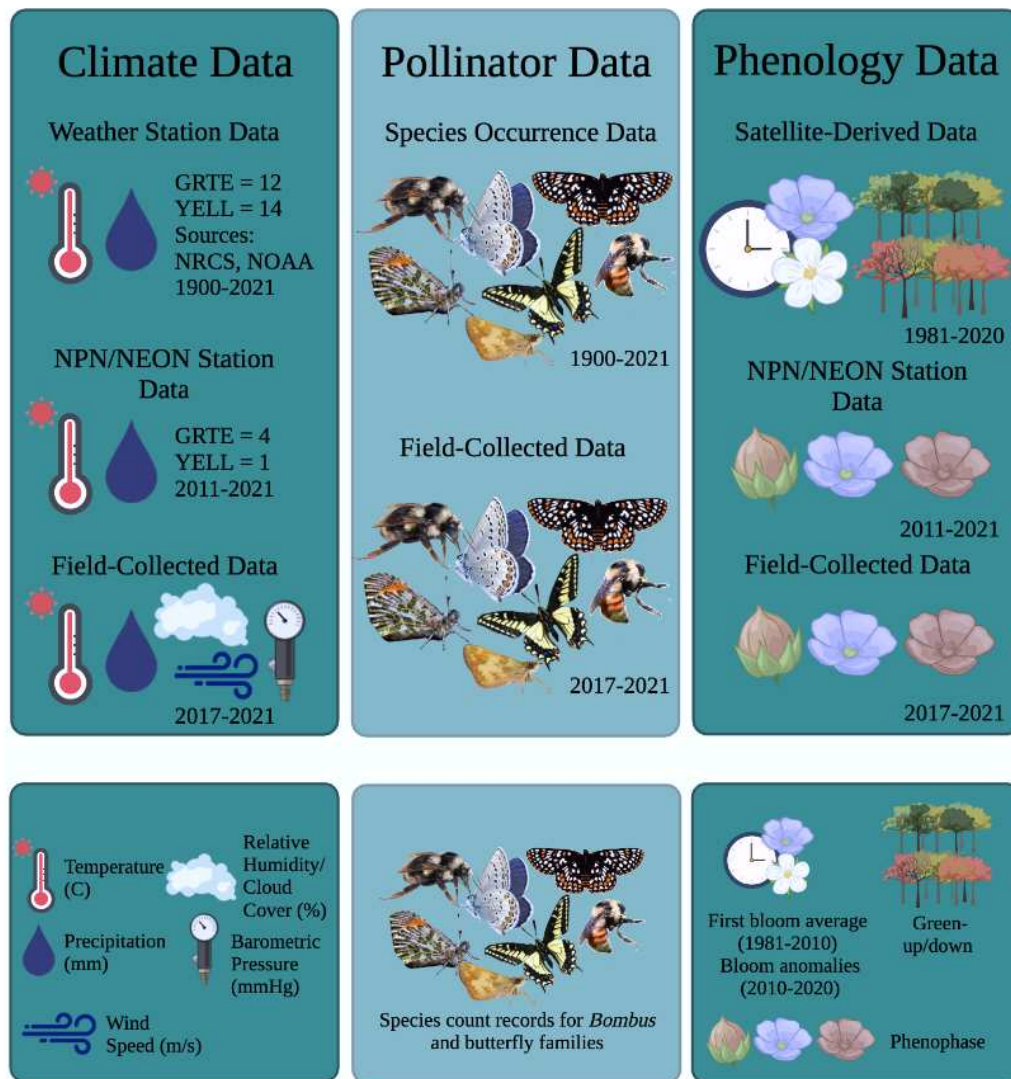
Figure 3.2. Data materials used for this research, including climate, pollinator, and floral phenology datasets. For climate data, records originated from weather stations as well as field collections. For pollinator data, records originated from species occurrence datasets (including museum collections and citizen science observations) as well as field collections. For phenology data, records originated from satellite data, station data, and field collections. Across all the datasets, there were slight variations in the temporal data availability.

3.1 Climate dataset preparation

To understand variations in phenology and pollinator emergence, climate data (temperature and precipitation) were queried from 1900-2021 from the National Oceanic and Atmospheric Association (NOAA) (NOAA, n.d.) and Natural Resources Conservation (NRCS) SNOTEL data sites in and surrounding Yellowstone (12 sites) and Grand Teton (11 sites) (USDA NRCS, n.d.). These stations vary across elevations and subsequent habitat types and act as strong correlating variables in relation to bloom dates and anomalies seen across the sampling period, as well as in relation to pollinator occurrence records. Generalized climate trends, including average temperature and precipitation, were compiled in conjunction with pollinator seasonal patterns on an annual scale during the growing season (April--September), or the peak green-up season for the area in which pollinators could be in flight (Hostetler et al., 2021; Notaro et al., 2019). Climate records were pulled at the earliest start date available for each park, starting from 1900 for Yellowstone and 1910 for Grand Teton. These values were compared to the findings of the GYE Climate Assessment, which included average changes in temperature, precipitation, and snowfall across regional watersheds and the entire ecosystem, to validate that climate station record trends were equivalent to the larger climate report findings available for the area (Hostetler et al., 2021).

3.2 Phenology dataset preparation

Phenology data were downloaded for both GRTE and YELL from the US NPN and the National Ecological Observatory Network (NEON) using NPS areas of analysis (AOA) that contain park boundaries and areas 30 kilometers surrounding the park (USA-NPN National Coordinating Office, 2021; NEON, 2022; NPS Natural Resource Inventory and Monitoring

Division, 2021). Both the NPN and NEON follow the same standardized protocol produced by the NPN for phenophase data collection, and the availability of data across the parks were based on site origination from the respective agencies. Historically, the NPN and NPS have had long-term ties for data collection and phenological monitoring (Rosemartin et al., 2021); hence, this data repository acts as the primary source for park-wide observational data.

Phenology data were available in two formats from NPN: satellite-based data and NPN/NEON observational data. Data were downloaded for historic first bloom periods from 1981-2010 and first floral bloom anomalies from 2011-2020, both of which originate from satellite-derived datasets. The 30-year normal bloom onset provides a range of spatial variation in average bloom onset days for the AOA. Historic anomalies for the previous ten years indicate whether the weighted mean onset for each year was earlier (negative days) or later (positive days) than the 30-year normal. In addition, the NPN provides historic estimates of mid-green-up and mid-green-down dates derived from MODIS satellite data. These values represent the day of the year of half peak greenness (green-up) and the day of the year halfway between peak greenness and senescence (green down). This data complemented the NPN/NEON monitoring site phenophase observational status data available from 2011-2021, which documented plant phenophase statuses throughout the growing season in addition to climate (temperature, precipitation) metadata (Figure 3 includes NPN/NEON site locations).

3.3 Pollinator dataset preparation

Pollinator (bumble bee and butterfly) records from NHCs, citizen science platforms, and NPS research permit reported specimens were downloaded from online databases from 1900-2021 (Whipple et al., 2023). Species were filtered by location, a 60-kilometer bounding box

containing the two parks and surrounding GYE area, then by the respective taxonomic level. Within butterflies, species were individually filtered based on the five dominant butterfly families observed within the park: Hesperiidae (Skippers), Lycaenidae (Blues and Hairstreaks), Nymphalidae (Brush-footed Butterflies), Papilionidae (Swallowtails), and Pieridae (Whites, Sulphurs, and Yellows). Bumble bees (genus *Bombus*) were prioritized given the taxonomic accuracy possible within citizen science datasets compared to other bee and critical pollinator species groups like flies (MacPhail et al., 2020; Falk et al., 2019; Kremen et al., 2011; Mason & Arathi, 2019). Datasets with relevant records included: the Global Biodiversity Information Facility (GBIF) (GBIF 2022a, 2002b, 2002c, 2002d, 2002e, 2002f), the Symbiota Collections of Arthropods Network (SCAN), iNaturalist, the Smithsonian Institution, the Lepidopterist's Society, BugGuide, *Bombus* of Canada, the Yellowstone Heritage Research Center, private collections provided by the C.P. Gillette Museum of Arthropod Diversity, Yellowstone's Fourth of July Butterfly Count records (Marilyn Lutz, NPS, Joshua Tree, CA, personal communications, September 30, 2018), and iDigBio. All data was prepped using the "tidyverse" package in R (Wickham et al., 2019).

3.4 Field sampling collections: climate, phenology, and pollinator data

Field crews sampled 21 sites across the GYE in sagebrush, meadow, and subalpine habitats. Sites were selected based on elevational ranges that impact pollinator species diversity, as well as based on previous research plots defined by the park's long-term climate monitoring program, to reflect previous research sites (Bowser, 1988), or with the support of other park researchers (Erik Öberg and Anne Rodman, NPS, Yellowstone National Park, WY, personal communications, May 25, 2017) (Michael Dillon, University of Wyoming, Laramie, WY,

personal communication, June 1, 2017) (Figure 3.3). For more details on sites across the parks, including the number of sampling efforts, habitat type, and years sampled, see Appendix C1. During each visit, field crews spent about two hours per site depending on locational terrain, weather, and species present for the day. Surveys were only conducted during optimal pollinator flight conditions: between 9:00 and 17:00 with temperatures between 24-38 °C, less than seven meters per second wind speed, and less than 30% cloud cover (Robinson et al., 2012). Surveys were completed during the average floral bloom periods for the area, from late May to late August, with peak sampling efforts from mid-June to late July.

At each site, researchers surveyed climate, phenology, and pollinator data. Field crews documented climate variables including temperature (°C), wind speed (m/s), relative humidity (%), barometric pressure (mmHg), and cloud cover (%) at the beginning and end of each field sampling period using a weather kestrel and/or a HOBO weather station (Kestrel Instruments, n.d.; Onset Computer Corporation, n.d.). This validated observation days that were higher or lower in species presence and to follow the recommendations for optimal sampling conditions (Robinson et al., 2012). Phenology observation records included the floral species family, common name, percent coverage of the sampling area, phenophase of each species, plant location within the sampling area, and any other notes to connect resources back to photographs taken.

Field crews used Pollard walks to observe pollinator species richness and evenness across the varying habitat types with mixed field crew support (Pollard, 1977; Royer et al., 1998; Pellet et al., 2012). Surveys were completed using the EpiCollect5 platform, a cloud-based data collection application where project data can be publicly accessed. Pollinator collection records included the species functional group (bumble bees versus butterflies or other insect species),

species scientific name, number collected, species description including color and pattern, wing wear, and capture location (on a plant, flying, or on the ground). All pollinator observations were catch-and-release; specimens were captured, cooled on ice for approximately 10 minutes, photographed using high resolution macro-lens cameras, and then released. To make accurate species identifications, field crews used resources for bumble bees from Koch (2012) and for butterflies from Debinski and Pritchard (2002), Poole (2009), and a personal guide created by Whipple and Opler (2018). All photographed observations (floral resources and pollinators) were uploaded and confirmed by other citizen scientists within the iNaturalist database for accurate species identifications. iNaturalist hosts all data collected due to its increasing participatory support, improving accuracy, and importance within public land conservation efforts (Dennis et al., 2017). As a result, all pollinator observations completed by field crews were included in the overall pollinator records used in this study.
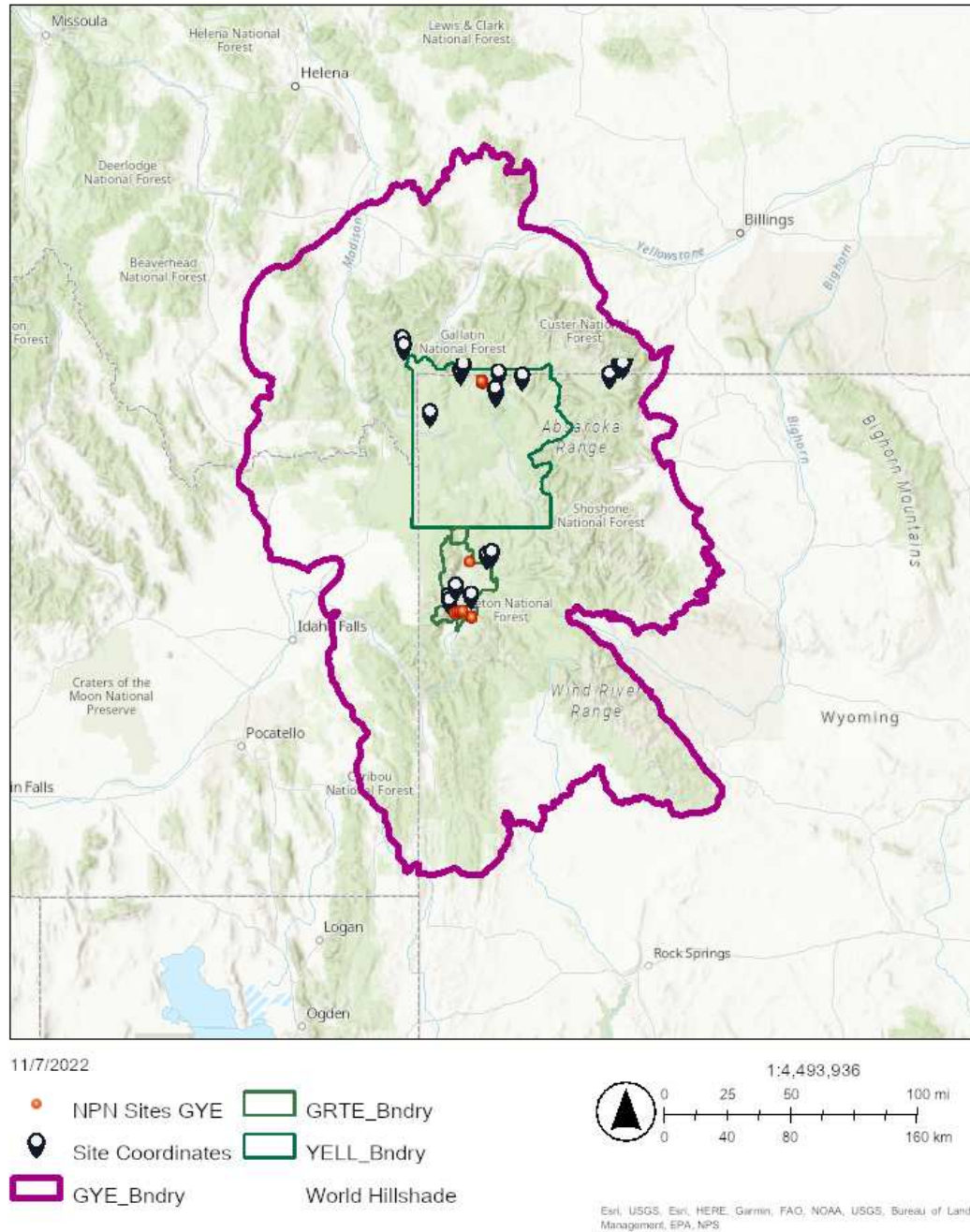
Figure 3.3. Sampling locations within GRTE, YELL, and the surrounding GYE, represented by black pins. NPN/NEON sites represented by red dots. For additional details on site sampling locations, including sampling years and number of visits, see Appendix C1.

3.5 Bloom averages, anomaly, and NPN/NEON observational data analysis

Phenology data from NPN/NEON were assessed first for spatial trends in historic

growing periods (1981-2010) and in relation to recent bloom anomalies (2011-2020) using the

satellite-derived datasets. All satellite data were analyzed using the "rnpn" package (Rosemartin

et al., 2022). Bloom anomaly deviations from satellite data were used to understand changes in

the first bloom date across field sampling sites. Field sites with multi-year sampling efforts were

prioritized in this analysis to assist in the data validation of field-sampled phenology records.

Next, an unequal variance t-test (Welch's t-test) was used to understand if the change in bloom

date was significant over time across both parks (Welch, 1938). The NPN/NEON observational

data was then visualized to understand the relationship between Julian Day of the Year and

phenophase stages across floral categories: early spring, mid-summer, late summer, non-native,

and berry-producing species. In addition, a Kruskal-Wallis test and pairwise Wilcoxon test were

used to understand the relationship between floral category phenophase groups and emergence

dates (McKight & Najab, 2010). P-values from these tests were adjusted using the Bonferroni

correction method.

3.6 Field-sampled pollinator/phenology/climate analysis

To understand the effect of phenophase/floral emergence patterns on pollinator species

occurrences, a Pearson's correlation test was used to compare phenophase stages (budding, half-

bloom, bloom, and senesced) on pollinators observed within each habitat type. Correlation tests

were performed to help translate plant-pollinator results in relation to broader phenology

monitoring efforts, such as NPN/NEON status datasets. Finally, to determine the effect of

climate on pollinator occurrence and floral phenology, principal component analyses (PCAs)

were run across GRTE and YELL datasets. The PCA used a combination of all available pollinator data (NHC, citizen science, and field records), phenology data (NPN/NEON and field records), and climate data (station-derived and field records) to interpret any association of patterns occurring over time. Given historic pollinator data availability on the monthly and annual scales, bumble bees and butterflies were lumped together for this analysis to understand general patterns of pollinator species occurrence in relation to climate variations. PCA analyses and plots were completed using the R packages "FactoMineR" (Husson et al., 2016), "factoextra" (Kassambara & Mundt, 2017), and "corrplot" (Wei et al., 2017).

4. Results

4.1 Phenological trends

Satellite-derived data indicated that for GRTE, the bloom date ranged from May 31-July 9, with a median onset of June 20. The estimated core green season from 1981-2010 was June 6-September 11. For YELL, the 1981-2010 bloom date ranged from May 24-July 13, with a median onset of June 26. The estimated core green season from 1981-2010 was June 7-September 12. Variations in bloom dates were observed across the latitudinal gradients of the parks, as well as elevational gradients that impact other climate variables and subsequent species emergence.

First flower averages from the satellite-derived datasets were queried for field sites and compared to recently observed bloom anomalies from 2011-2020 (Figure 3.4). First flower blooms from 2011-2020 have occurred three days earlier compared to the 1981-2010 average, with variations seen across sites along the elevational gradients. For example, in YELL, the top of Mount Washburn has observed flower blooms five days earlier than historic averages, while Mammoth Hot Springs has observed flower blooms two days earlier. In GRTE, Death Canyon

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and Granite Canyon have both observed flower blooms three days earlier than historic averages. The unequal variance/Welch's t-test comparing the difference between first flower bloom averages and recent bloom anomalies indicated a non-significant difference between historic bloom dates and current anomalies (p-value=0.4623) (Table 3.1).
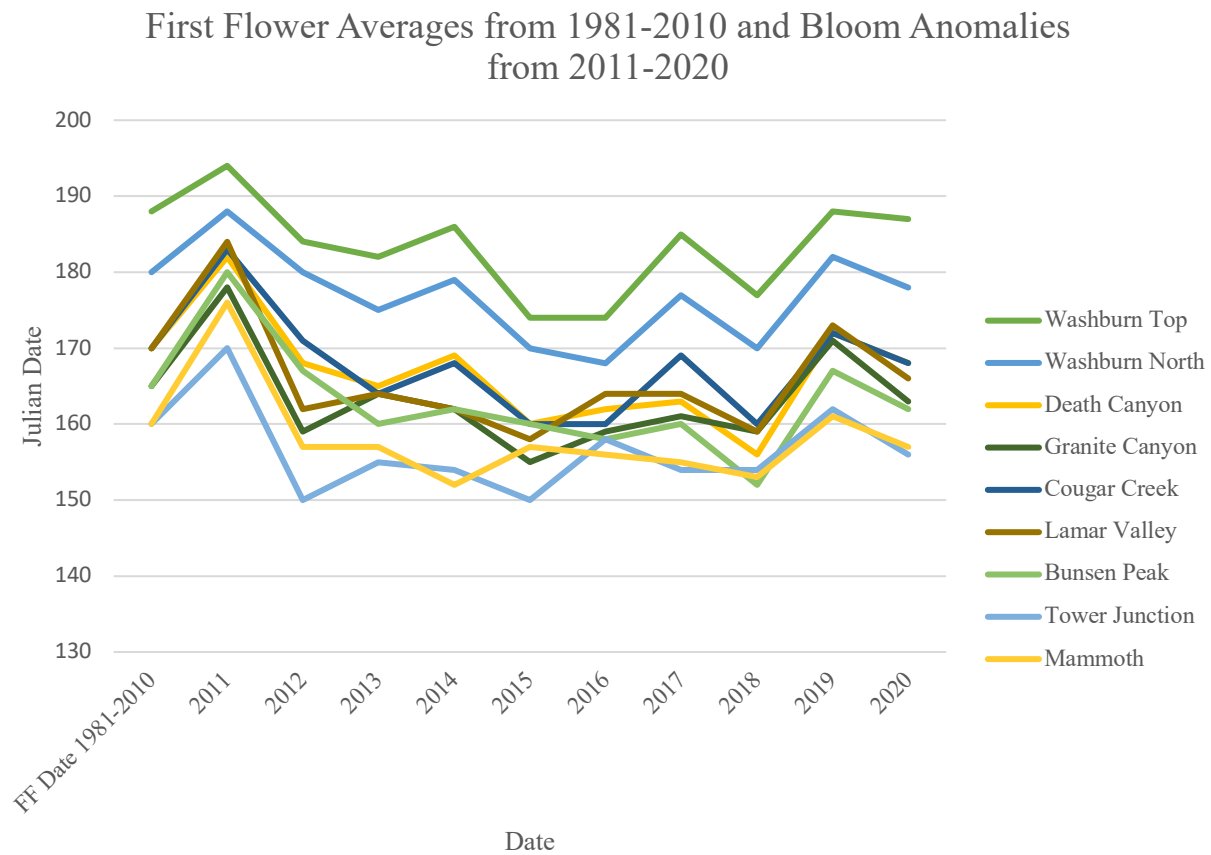
Figure 3.4. First flower averages from 1981-2010 and the change in first flower days from 2011-2020 (bloom anomalies) across field site locations, as indicated by Julian Day of Year. Data acquired through US-NPN satellite-derived datasets.

Table 3.1. Welch's t-test at the 95% confidence interval comparing difference between first flower averages from 1981-2010 and bloom anomalies of first flower dates from 2011-2020.

t statistic	df	p-value
0.75327	15.914	0.4623

Within the status and intensity data, variations in phenophase periods across the floral seasonality categories occurred (Figure 3.5). Early spring and non-native species phenophase periods, as well as variation across periods, were most similar, whereas mid- and late-summer species observed similar trends in phenophase periods. Early spring species had the most spread across Julian days within all phenophase stages. In contrast, late summer species had the least variation across phenophase stages. Berry-producing species observed the most outlier observations in phenophase periods across the growing season. To validate these variations, the Kruskal-Wallis test indicated strong significance between the Julian day period and floral seasonality ($p < 0.005$) (Table 3.2). The pairwise Wilcoxon test indicated some level of significance between all floral seasonality paired groups ($p < 0.05$) (Table 3.2). For a complete list of floral species observed by NPN/NEON sites, see Appendix C2.
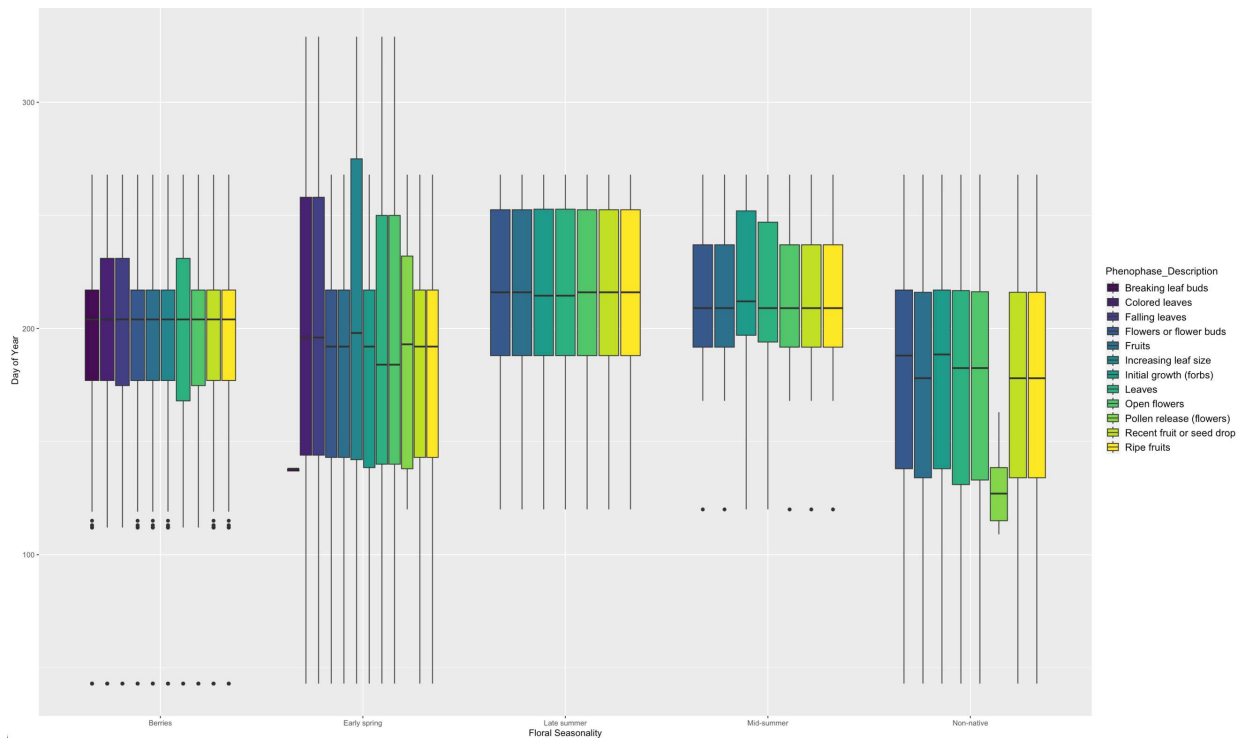
Figure 3.5. Box plot representing seasonality in relation to Julian day (day of year) for NPN/NEON sites by phenophase stages. Seasonality definitions for floral resources were defined by Bloom et al. (2022). For a list of floral resources collected at NPN/NEON sites and their seasonality category, see Appendix C2.

Table 3.2. Kruskal-Wallis test, and pairwise Wilcoxon test results to understand the relationship between Julian day emergence and floral seasonality. The relationship between late summer and berry/early spring species, between mid-summer and early spring species, and between non-native and all species categories were considered significant. P-values <0.001 are denoted with two asterisks (**); p-values <0.0001 are denoted with three asterisks (***).

Kruskal-Wallis Test		
$\chi^2 = 129.71$	df = 4	p-value = 2.2 x 10^{-16}***

	Berries	Early spring	Late summer	Mid-summer
Early spring	0.65	-	-	-
Late summer	5.5 x 10^{-9}***	3.8 x 10^{-5}***	-	-
Mid-summer	0.0003***	0.004**	0.39	-
Non-native	< 2 x 10^{-16}***	< 2 x 10^{-16}***	< 2 x 10^{-16}***	< 7 x 10^{-13}***

4.2 Field-sampled pollinator/phenology/climate trends

Pearson correlation statistics found that there was a significant effect on pollinator occurrence in relation to phenophase stages (Table 3.3). For all three habitat types, there was a positive, significant species occurrence response to senesced plant occurrence. The meadow and subalpine habitats also observed a significant, negative response to the occurrence of half-bloomed plants. Budding and full bloom phenophase stages had no significant effect on pollinator occurrences; however, budding resources had a slight negative correlation with species occurrences in sagebrush and meadow habitats, while full bloom resources had positive correlations with species occurrences across all habitat types.

Table 3.3. Correlation statistics between pollinator occurrence and phenophase stages across habitat types. The relationship between half-bloom and senesced floral resources in relation to pollinator occurrence showed mixed levels of significance across habitat types. P-values <0.05 are denoted with an asterisk (*).

	Sagebrush p-value	Sagebrush correlation	Meadow p-value	Meadow correlation	Subalpine p-value	Subalpine correlation
Budding	0.63	-0.09	0.48	-0.08	0.50	0.16
Half-Bloom	0.38	-0.17	0.03*	-0.23	0.05*	-0.44
Bloom	0.55	0.11	0.24	0.13	0.95	0.02
Senesced	0.04*	0.37	0.0008*	0.35	0.004*	0.61

The PCAs for climate, phenology, and pollinators indicated strong relationships between climate variables and phenology/pollinator responses. Across all three datasets, the first three principal component (PC) dimensions represented 50-60% of the explained variance (Figures 3.6A-3.8A). For the NPN/NEON phenology datasets alone, park location (indicated by latitude and longitude), Julian day, and month had the strongest effect on the variance within PCA (Figure 3.6 A&B). GRTE data indicated strong variation and correlations with sampling year, temperature, total occurrence, and the butterfly family Nymphalidae total occurrence and richness values (Figure 3.7 A&B). Nearly all species occurrence and richness values were moderately to strongly correlated with sampling year, while only the genus *Bombus* showed a correlative response to sampling month in both occurrence and richness values. Genus *Bombus* was the only species group to show minimal response to temperature; all species groups except for family Nymphalidae had some response to precipitation. YELL data indicated strong variation and correlation with the total number of family Lycaenidae and Pieridae occurrences in response to the sampling year (Figure 3.8 A&B). All additional species occurrence and richness values had some level of correlation to the sampling year, but not as strong of a response. Much like GRTE, genus *Bombus* species occurrence and richness values were correlated to sampling month; families Hesperiidae and Pieridae also showed minor correlation. Temperature values correlated to genus *Bombus* occurrence and richness totals, as well as Nymphalidae and Papilionidae richness totals. Precipitation values correlated to family Hesperiidae occurrence and richness totals, as well as Lycaenidae, Papilionidae, and Pieridae totals.
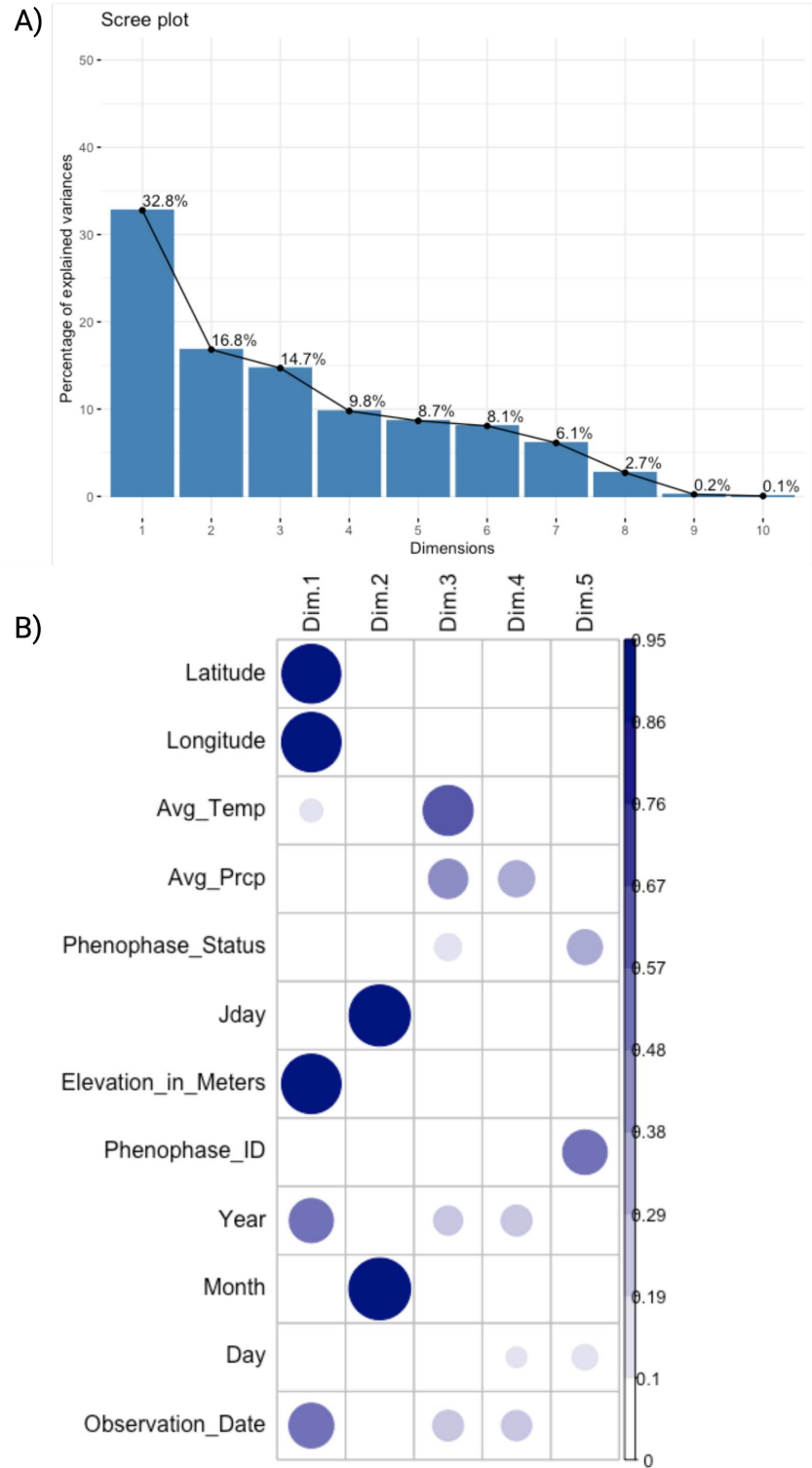
Figure 3.6. A) Scree plot of eigenvalues for phenology PCA to determine the effect of variation across dimensions. B) The phenology/climate correlation matrix for the top five dimensions that account for over 80% of the PCA variation. Larger circles and darker colors represent stronger correlations amongst PCs. For example, in dimension 1 (Dim1), latitude, longitude, and elevation are strongly correlated.
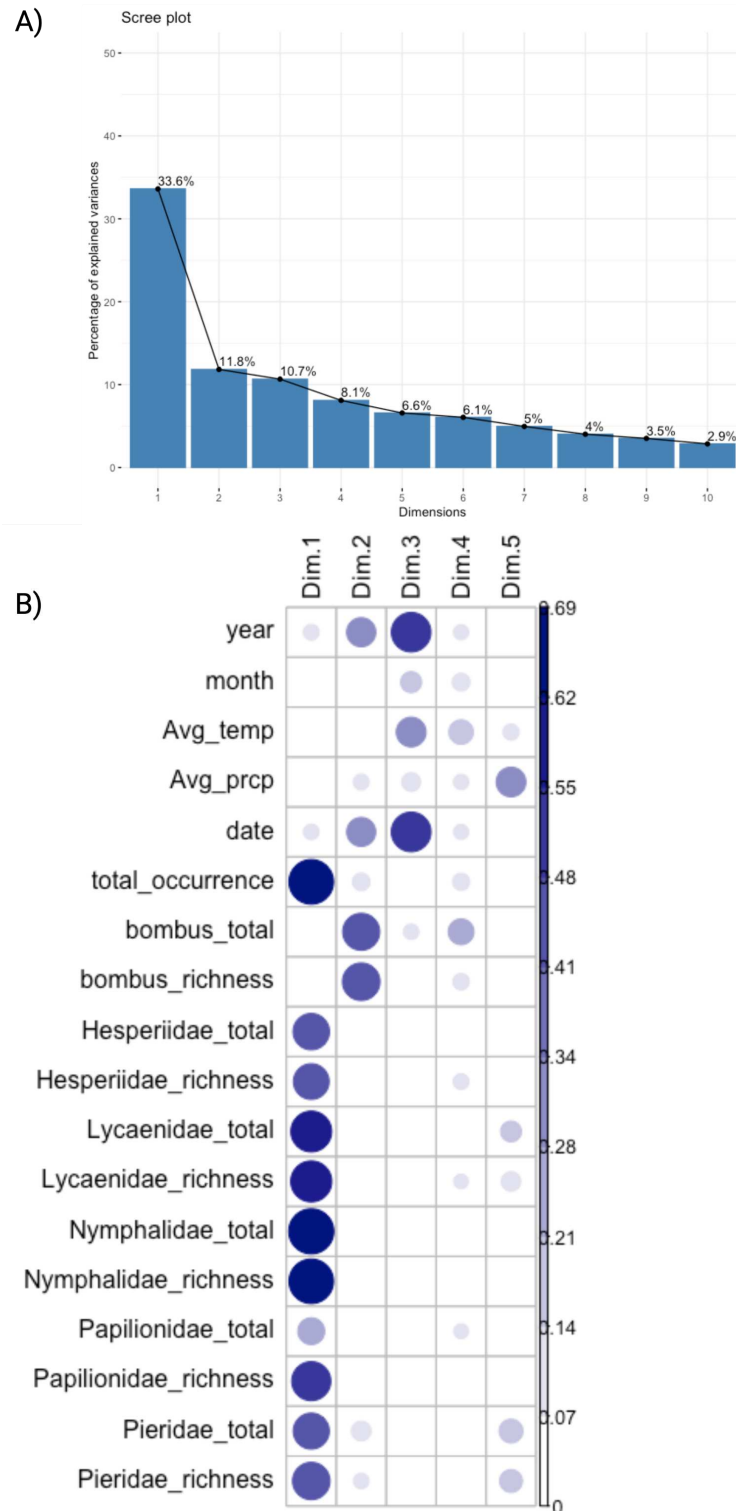
Figure 3.7. A) Scree plot of eigenvalues for GRTE PCA to determine the effect of variation across dimensions. B) The pollinator/climate correlation matrix for the top five dimensions that account for over 80% of the PCA variation. Larger circles and darker colors represent stronger correlations amongst PCs. For example, in dimension 1 (Dim1), total occurrence and all species groups are strongly correlated.
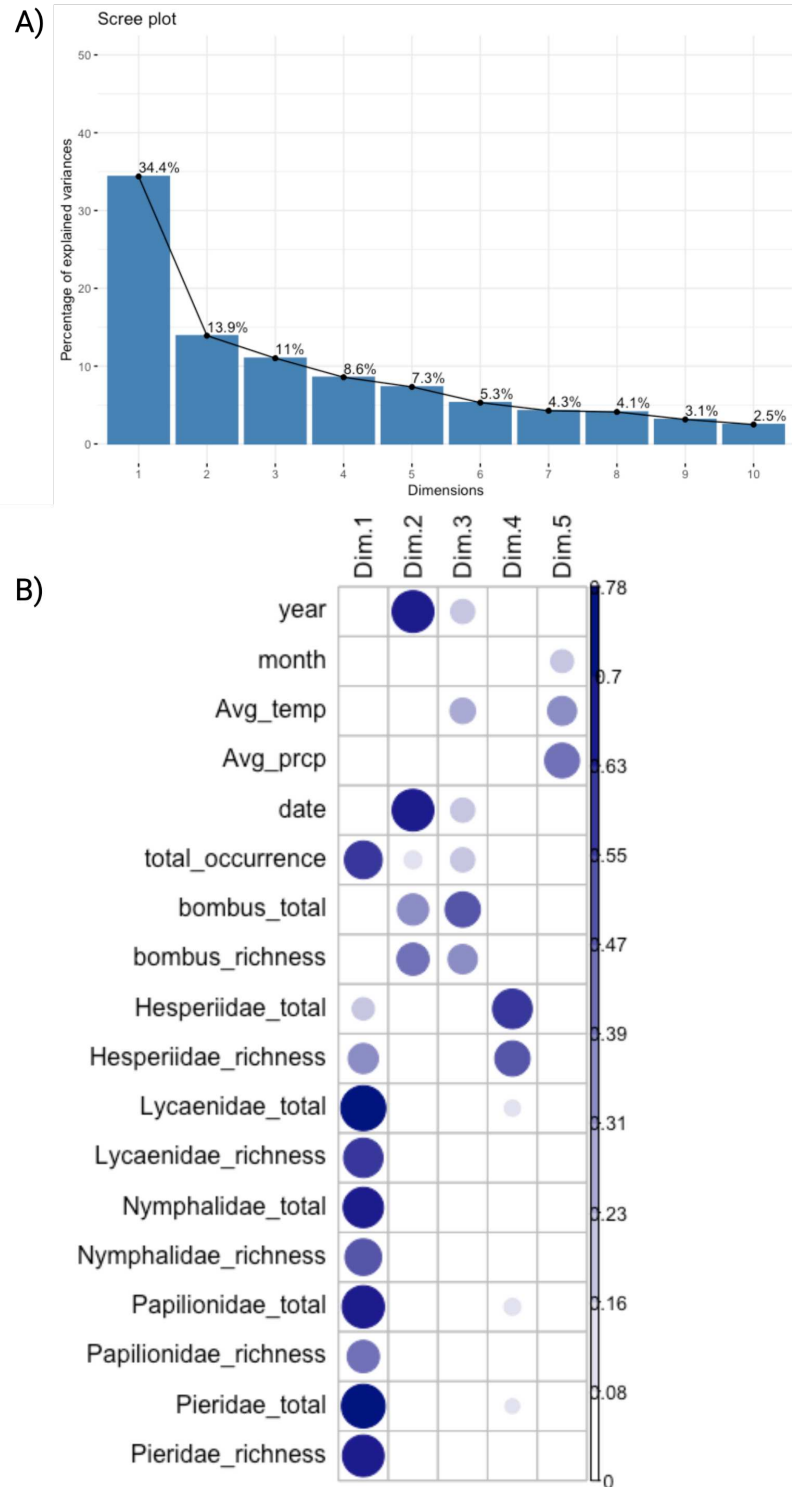
Figure 3.8. A) Scree plot of eigenvalues for YELL PCA to determine the effect of variation across dimensions. B) The pollinator/climate correlation matrix for the top five dimensions that account for over 80% of the PCA variation. Larger circles and darker colors represent stronger correlations amongst PCs. For example, in dimension 1 (Dim1), total occurrence and all species groups are strongly correlated.

5. Discussion

GRTE, YELL, and the GYE have experienced unprecedented changes in climate since 1900, yet pollinator and floral phenology responses to these changes are less prominent. While researchers have tracked the change in first-floral bloom dates over time (Bloom et al., 2022), satellite-derived data from NPN indicated that recent bloom anomalies were not significantly different from the previous 30 years (Table 3.1). With additional data collection efforts, I found that slight variations in phenophase stages and emergence patterns across floral groups occurred in both parks, specifically within the berry, early season, and non-native floral groups (Table 3.2). This means that, in the event of a phenological mismatch in the future, pollinator species may have seasonally diverse floral resources available. These findings highlight the need for additional sampling efforts, particularly across the growing season, to better understand the nuances seen amongst floral groups that may subsequently determine pollinator activity.

The observational data availability across the parks varied; in GRTE, the NPN sites have been sampled since the early 2010s, but in YELL, the NEON sites were formally established in 2018. While both agencies use the same phenology and climate data collection protocols, the temporal variation leads to greater uncertainties in the phenological patterns observed within YELL. To answer broader questions of phenological change across both parks, considerations towards data standardization, including the sampling frequency, species of prioritization, and site selection, needs to occur. The satellite-derived datasets provide an additional, standardized effort observed across not only the two parks but nationwide; these efforts should continue to act in tandem to provide the most accurate understanding of phenological change at a coarse and fine-scale site resolution.

The Pearson's correlation statistics found positive and negative relationships between pollinator occurrence and the different phenophase stages, which indicates varying levels of phenological synchrony and desynchrony (Table 3.3). Budding resources did not significantly affect species occurrence, but these resources had negative responses on species occurrence in all habitat types except for the subalpine areas. Half-bloomed resources were only significant in their effect on pollinator occurrence within the meadow and subalpine habitats and had a negative correlation in all habitat types. Interestingly, senesced resources were significant across all habitat types and showed a positive correlation. These patterns offer speculation, such as the species resilience of pollinators across habitat types. Within plant-pollinator interactions, researchers predict that species that are resilient to phenological changes will be more likely to persist than those who will maintain restricted ranges of emergence (Polgar et al., 2013; Biesmeijer et al., 2006). Resilient species may also include non-native plant or insect species that could outcompete specialist or native species for floral rewards; however, little data on the impact of this resource phenomenon has been reported (Giejsztowt et al., 2020). The floral resource phenology/pollinator relationships speak to the resilience of species found across all habitat types, but the most alarming results were found in the subalpine habitat species (negative budding, non-significant; negative half-bloom, significant; positive bloom, non-significant; senesced, significant). Additional studies, such as more precise research into species' movement along the habitat/elevational gradient, will offer more indications on these interactions.

However, there were no field sampling efforts in which a site had no floral resources present or floral species present that were all senesced. Because mountains are heterogeneous landscapes, the spatial variation of field sites present, even among microhabitats, may present more favorable resources nearby that could skew the species observed (Rahbek et al., 2019;

Auckland et al., 2004; Inouye, 2019). Additional sampling efforts, particularly within the early season or late season period that could capture greater variations in budding and senesced resources, may better inform these relationships. Studies that also look at specialized plant-pollinator relationships in the GYE, particularly those that emerge earlier in the growing season, may elucidate different species responses as well.

The influence of climate on floral phenology and pollinator species occurrence within GRTE and YELL may indicate that temperature and precipitation changes observed within the area have impacted both species groups from 1900-2021 (Figures 3.6-3.8). Floral phenophase stages were slightly correlated to temperature and precipitation, but other variables, such as elevation and site location, showed stronger correlations within the PCA. Unlike temperature and snowpack, precipitation has remained relatively consistent in both parks over the climate monitoring period (Hostetler et al., 2021), which may account for the little effect that this has had on floral species over time. While precipitation is not typically the primary driver of phenological shifts and ambient air and soil temperatures are considered the most informative, researchers agree that additional studies within systems with changing precipitation regimes need to occur (Bartomeus et al., 2011; Lesica & Kittelson, 2010). These dynamics may be important in the GYE as precipitation is anticipated to transition from more snow to rain, and across different seasons (Hostetler et al., 2021).

Patterns of correlation for pollinator occurrence across both parks were relatively similar, yet the strength of the correlation slightly varied. There was a stronger correlation between sampling years and total available records (total occurrences) in GRTE, yet both parks had strong correlations with time across all species groups. This may be a result of greater citizen science efforts in recent years, or the rate of digitizing more recent NHCs (Whipple et al., 2023).

Temperature affected genus *Bombus* the most between both parks, with a slightly stronger response in YELL, whereas precipitation affected genus *Bombus* in GRTE and Hesperiidae, Lycaenidae, Papilionidae, and Pieridae in YELL. The interactions between climate and time variables had a stronger effect for GRTE species than YELL. This difference may be tied to the seasonality of the pollinator records available. There was a greater spread in records available across the growing season (April-September) in GRTE than YELL, and early versus late emerging species may be important indicators in community dynamics (Parrish & Bazzaz, 1979) or species observations available over time. Additionally, the GYE spans elevational gradients from approximately 1,219 to 4,000 meters (with a greater elevational spread in GRTE), and these variations in locational trends made a difference in the species assemblages observed (Hostetler et al., 2021; Romme & Turner, 1991).

Forrest (2014) argues that, given the "multivariate nature of climate change," questions related to large-scale, observation-based pollinator decline will be hard to answer without more targeted approaches. This study offers opportunities to assess how known climate shifts in the GYE have previously impacted species occurrence, but additional understanding in relation to stronger floral phenology datasets will strengthen these findings, as will more targeted sampling efforts in areas most susceptible to accelerated climate change effects and within the early and late season growing periods. As climate extremes worsen for the area as projected, species dynamics may change. Therefore, close, standardized monitoring of pollinator-plant relationships and changing climates needs to occur.

6. Conclusion

In this study, we demonstrated plant-pollinator interactions occurring among varying habitat types within the GYE are dependent on specific phenophase stages and climatic conditions. Given the nature of the GYE, which spans diverse elevational gradients and habitat types that experience variations in phenological phases (Rykken et al., 2014), as well as the knowledge of a changing climate that will impact species distributions over time (Hostetler et al., 2021; Hansen & Phillips, 2018), this study leveraged data collected from various sources (such as citizen science applications and virtual datasets in tandem with field observational studies) to answer critical questions such as pollinator decline, climate change, and phenological shifts to the protected areas seen within the GYE. Together, research findings can extend beyond the GYE in their implications for the state of pollinator diversity within the US and the effects that climate change may have on pollinators and phenological patterns observed within protected areas. Nonetheless, more research is needed to understand these shifts and the phenological responses of plant species, particularly within the early and late season timeframes in which the greatest climatic variation is anticipated.

CHAPTER 5: CONCLUDING REMARKS

1. Discussion

The following research efforts provided an understanding of pollinator, floral phenology, and climate data in Grand Teton (GRTE) and Yellowstone (YELL) National Parks through three studies and their takeaways. These takeaways are summarized in a conceptual diagram (Figure 5.1). To understand these patterns at the global scale and provide translations to the future status of species, the first study used a meta-analysis approach to generalize the overall patterns of species responses to climate change. Across all literature, temperature acted as the primary climate driver for species responses. While bumble bee data was limited in nature, some findings, such as species' range contractions and phenological mismatches between floral resources, were found with medium-to-high agreement. The butterfly datasets had more literature available, but this did not lead to higher confidence in observed trends. The response of species' generalists (increasing), as well as the pattern of earlier emergence trends, had the strongest agreement with medium evidence. In contrast, butterfly research highlighted more of the land-use effects than any bumble bee literature provided, which grants opportunities for future studies to consider the coupling of climate change with land-use change.

Next, the data behind pollinator occurrence records in the GYE were assessed to not only highlight prioritized species within research efforts and collections, but also to address the underlying taxonomic biases and data gaps present within the databases themselves. The parks were well-represented in historic and recent occurrence data, but with strong taxonomic biases. In addition, the transition of data from Natural History Collections (NHCs) to citizen science applications could be an effect of museum digitization backlogs or due to the rising community present on citizen science platforms. Private collections were informative for some species

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groups (Hesperiidae) that lacked data among other platforms and locations; however, the trade-offs between database types limited the efficacy of species comparisons amongst datasets. Collections, citizen science applications, and private/permit-derived data nonetheless highlighted a handful of taxa that researchers can use as occurrence baselines for future species conservation monitoring, despite the taxonomic and database biases present.

With this data context in mind, the final study incorporated floral phenology and climate data metrics to understand the effect of climate change, in the form of temperature and precipitation changes, on floral phenology and pollinator occurrence patterns. Floral bloom periods have occurred on average three days earlier since the 1980s, but this earlier occurrence was non-significant and varied across park locations. More defined variations in phenology happened amongst seasonal floral groups, with some observed overlaps between species, particularly in early season, non-native, and berry groups, that were significant. The plant-pollinator studies found that species were more affected by early and late-season phenophase stages, which offers indications for species to prioritize in future studies and those in which there may be synchronizing or desynchronizing effects from floral resources. When combined, the effect of climate on pollinator and floral phenology patterns showed mixed effects, but none of significance. The effect of temporal variation had a larger impact on species occurrence than temperature and precipitation; however, pollinator groups, such as the varying butterfly families observed in the park, responded differently and with varying relationship strengths.
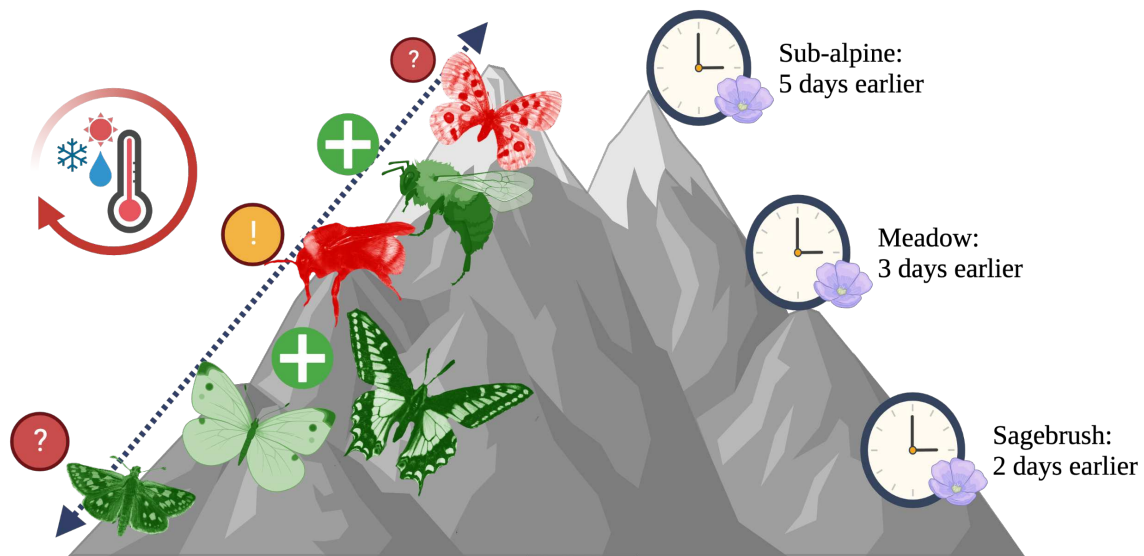
Figure 5.1. Conceptual diagram representing my research findings and translated to the GYE. These include: the importance of parsing out species responses to climate variation, the effect of climate variation on floral phenology and pollinator occurrence, and how, given data availability and taxonomic biases, species status assessments under climate scenarios may come with greater uncertainty.

1.1 Lessons learned

1. Diversity amongst species groups led to variations in species responses. Pollinator species will respond inconsistently to climate and land use pressures, and this makes future

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predictions difficult to agree upon. Some findings were more evident, such as the range contractions observed amongst bumble bees worldwide, or the varying responses between species specialists and generalist butterfly populations with changing climate and landscape pressures. Bumble bees and butterflies face the risk of phenological mismatches between floral resources. These findings complement the work done within the GYE by re-emphasizing the complexities of species behavioral strategies, floral resource preferences, and local species adaptations. Nevertheless, the integration of land use change, as more commonly observed in the butterfly literature than the bumble bee studies, may help to understand these species responses in greater detail.

      2. Database uncertainty mattered. To answer any questions centered around topics such as biodiversity loss and climate change, a robust understanding of the status of species is necessary, but this requires an understanding of the data origins that generated such conclusions. While the data available for the GYE was sufficient to answer baseline questions on some taxonomic groups, there were taxonomic biases and systematic gaps between data rescue, digitization/availability, and management/archiving across database types. Additionally, the taxonomic priorities of previous researchers emphasized a handful of functional groups, but this led to greater uncertainty on the status of less observed species. Citizen science could play a role in spreading efforts across temporal and spatial scales and in broadening observed taxa; the evidence of new tools such as citizen science applications acted as the primary cause for an influx in species occurrence data more recently. These platforms may not be informative for lesser-studied taxa or those that require additional identification skills, but they proved to be sufficient for the species studied in this research (MacPhail et al., 2020; Falk et al., 2019; Kremen et al., 2011; Mason & Arathi, 2019).

3. The climate in the GYE has changed, but pollinator and floral species responses to such change are less clear. Climate variables (temperature and precipitation) had mixed effects on the occurrence of bumble bee and butterfly species as well as on floral phenology stages. The influence of time, with additional research efforts, had a stronger influence on species occurrence patterns than climate variables. Floral phenology emergence shifted on average three days earlier than was previously observed, but this varied across park locations and elevational gradients. Correlation analyses between pollinator and floral resources observed negative relationships in response to half-bloomed resources across all habitat types, and a positive relationship between senesced resources, all of which were significant. These patterns seem contradictory but may argue for the resilience of species observed within this ecosystem, specifically during the late bloom periods. Once again, more baseline evidence of general species occurrence could help to strengthen this understanding, as would additional phenology and climate monitoring efforts across elevational gradients.

1.2 Future research opportunities

Fill the taxonomic gaps. This effort worked to minimize taxonomic gaps across databases and park locations through the digitization of data. Even through these attempts, taxonomic biases occurred, even with the prioritization of sites to reflect species with greater diversity. Areas with low diversity matter, especially in the age of climate change, but these questions are more challenging to answer with the fraction of available data online. Accounting for species absences will be important as climate change accelerates land cover change over time, as will the continuation of baseline inventories to assess the status of all taxonomic groups that could then inform species management and broader conservation decisions.

Prioritize early and late emerging species, especially in relation to climate. Both

negative and positive, significant correlations were found between pollinator occurrences and

floral phenophase stages typically observed in the early and late growing seasons. However, this

research was limited in its studies within the spring and early fall time periods, when more floral

variation occurs. As a result, future efforts should consider observing these time periods in more

detail and with closer observations of the transitions between floral phenophase stages. This

could better inform the relationship between pollinators and floral resources and speak to the

resilience of species outside of peak resource availability. Additionally, spring temperature and

precipitation are anticipated to transform the most going towards 2100 (Hostetler et al., 2021), so

these dynamics may continue to evolve and act as justification for close monitoring as a result.

Pollinator species responses are and will continue to be nuanced, and therefore,

researchers need to consider the varying effects that climate change will have on taxonomic

groups. High-level assessments continue to lump biodiversity loss into species groups, and as a

result, such conclusions may be inaccurate or incomplete (Bertrand et al., 2006). The meta-

analysis found that bumble bees and butterflies varied in their responses to climate change

pressures, and land use change needs more consideration. In future biodiversity studies,

specifically those that target highly diverse groups like bees and butterflies, researchers should

consider speaking to the variances observed between taxonomic groups as this will be more

representative of the observed changes. These details will be more informative towards decision-

making processes, such as in advising species conservation or land management objectives, or in

prioritizing groups in which additional research efforts should occur.

Intact ecosystems, such as national parks, may make a difference for the future of

pollinator species diversity. GRTE and YELL are some of the fortunate parks in the US that

have a history of insect collections; many others lack data that would make these types of questions difficult to answer (Shafer, 1999). The parks are also fortunate to be connected through the GYE protective measures, as well as the even grander Yellowstone to Yukon Initiative that has helped in the conservation of many other species in the Rockies (Yellowstone National Park, 2022; Hostetler et al., 2021). Land connectivity and mitigating habitat fragmentation act as some of the strongest recommendations to minimize species loss in the age of climate change (Pörtner et al., 2022; IPBES, 2016). Harvey et al. (2023) reiterated the importance of conservation for insect diversity: "Insects will be more resilient to climate change when they consist of intact communities with high structural complexity and high levels of plant species diversity, which together will generate diverse micro-climatic refugia" (p. 18). Because the parks already benefit from such protective measures, this study reaffirms the continued benefit of ecosystem protection for pollinators, as evident through the minimal effect that climate change has had on known species occurrences. This also speaks to the resilience of the species and landscapes of the GYE, and the increasing importance of monitoring the effects of climate change on these species and landscapes over time. While other parks and protected areas may require additional baseline data collection prior to addressing these questions themselves, this study offers a foundation that can apply to other parks and protected areas through mechanisms that are publicly accessible and non-invasive.

1.3 Pollinator species vulnerabilities: three case studies for the GYE

Based on these results, data availability from the historic and recent sampling efforts, and plant-pollinator phenology patterns, I provide three species case studies for the GYE. Some pollinator species in the GYE already face potential decline (Graves et al., 2020), while others

are well documented and therefore may act as ecological indicators as climate change accelerates landscape change (Debinski et al., 2014). The western bumble bee (*Bombus occidentalis*), the fritillary taxa (*Boloria sp.* and *Speyeria sp.*), and the swallowtail taxa (*Papilio sp.*) have responded to climate change effects in differing ways across the western US and on the international scale. These case studies come with uncertainties but were included to help park managers and researchers consider species monitoring priorities that are applicable to other conservation goals, such as minimizing habitat deterioration or reducing invasive species encroachment. While these scenarios come with high uncertainty, the previous agreement and evidence collated from other researchers' data, in addition to my research findings and the lessons learned, amplify these claims.

Bombus occidentalis, a species of particular interest within the western US pollinator community (Graves et al., 2020; Janousek et al., 2023), had previous historic occurrences (765 out of 10,051 total *Bombus* records), within the digitized NHC and citizen science records available for the GYE (Whipple et al., 2023). Populations have sharply declined since 1990, much of which was correlated back to previously rich species records within museums and historic repositories (Thorp et al., 2009). Researchers found that the driving causes of decline for this species included increasing temperature, drought, and the use of neonicotinoids (Janousek et al., 2023). As a result, *B. occidentalis* was proposed for listing under the Endangered Species Act (ESA) back in 2015, and a decision on its status will be announced by 2023 (Thorp et al., 2009). More recently, Janousek et al. (2023) found that historic occupancy of *B. occidentalis* was highest in the GYE area and that under varying climate and land cover scenarios up to 2050, the species will face decline regardless of the intensity of change. However, the GYE may be one of the last remaining habitats the species occupies in 2050. In the past five years of sampling, field

crews observed *B. occidentalis* in six occurrences, all of which were validated as "research grade" on iNaturalist. While minimal in occurrences, this species may depend on protected, connected areas like the GYE to thrive, even amongst changing climates. Using both historic records to validate previous species presence and current tools such as citizen science data may ensure that critical species of concern like *B. occidentalis* are properly examined for conservation purposes.

The fritillary group (ten *Speyeria sp.* and seven *Boloria sp.*) acts as an understudied taxon in the GYE yet an important species group because they utilize specialized host-plant pollinator relationships with violets (*Viola sp*.) that may be impacted by changing landscapes. Through this meta-analysis, the literature prioritized species responses for declining fritillary species such as the Regal Fritillary (*Speyeria idalia*) (Henderson et al., 2018), but also for species that have expanded their range such as the Gulf Fritillary (*Agraulis vanillae*) (Halsch et al., 2020); neither of these species are observed in the GYE. Fritillary butterflies of GRTE and YELL tend to inhabit sagebrush and meadow ecosystems, two elevational gradients that face greater temperature and precipitation fluctuations going into 2100 (Hostetler et al., 2021). Violets prefer cooler, wetter habitats, which may be threatened as precipitation availability continues to decline with warmer temperatures. Previous work by Whipple et al. (2022a) found that fritillaries in the GYE preferred areas in the mid-elevational gradient, and citizen science documentation of both fritillaries and violets was robust enough to overlay species along species suitable habitats; even so, more data was available for both violet and fritillary species groups in GRTE than in YELL. However, as habitats change in response to climate variation, the previously suitable habitat of violets may change, and fritillaries will have to respond to such changes themselves or adapt to changing floral resource availability. The Mormon fritillary (*Speyeria mormonia*) had the

strongest historic occurrence records available for the park (Whipple et al., 2023) and therefore could act as an indicator species to define ecosystem integrity over time given its strong baseline data availability. Citizen science and virtual datasets could help to further refine the study areas of priority to monitor, and with an emphasis on the violet-fritillary relationship.

Swallowtails (seven *Papilio sp.*) are another group that has been understudied in the GYE but could respond to climate variation over time. While any increases in species richness over time are hard to document given the limited evidence in NHCs and citizen science databases, swallowtails are known to produce multiple generations in the event of favorable weather conditions (Hellmann et al., 2008). Conditions may not be favorable long-term (i.e., into 2100), but the short-term benefit of warmer temperatures and greater precipitation in the spring and fall may benefit species in the short-term; this pattern has been observed in Europe (Hellmann et al., 2008) and in the western US with other species (Crossley et al., 2021). Swallowtails are within the same family as the Parnassian butterflies, a group that has rich data available in the GYE and worldwide because of its habitat sensitivities and plant relationships (Debinski et al., 2014; Sbaraglia et al., 2022; Matter et al., 2011). Because family Papilionidae faces differing responses amongst individual species in this group, the continued documentation of these populations in the GYE may strengthen the understanding of their responses to climate and land use change within a relatively protected area over time.

2. Conclusion

This research started in 2018 with the intrinsic motivation and curiosity to answer biodiversity questions in National Parks using technology and citizen science tools. Fast forward to 2023, when this research transitions its objectives and produces results that show the

importance of parks for pollinator diversity and data discovery. GRTE and YELL have received special attention for over one hundred years, and the hope is that these ecosystems remain protected over the next century so that climate change effects are closely monitored, not only in their implications towards the bumble bees and butterflies but for all the species and wondrous ecosystems found in these special places. At the same time, the previous data has significant strides to go to ensure that collections help inform broader questions such as biodiversity loss and species resilience. While no one has the crystal ball that can accurately predict the status of pollinators, let alone the status of the planet as it continues to change, this research helps to bring optimism to the resilience of pollinator species present within the GYE. Now, these findings are reflected upon, interpreted to consider additional biodiversity, park management, and research needs, and acted upon to ensure that even the highly mobile and diverse pollinator species are closely monitored and protected for generations to come.

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APPENDIX A

Appendix A1. Literature available for bumble bee and climate studies.

Authors	Journal	Year	Focus taxa	Study location
Nascimento et al.	*Journal of Insect Conservation*	2022	*B. funebris*	Bolivia, Chile, Peru, Ecuador, Colombia
Sponsler et al.	*Ecology*	2022	*Bombus sp.*	Germany
Maihoff, F et al.	*Diversity and Distributions*	2022	*Bombus sp.*	Germany
Kudo & Ida	*Ecology*	2013	*Bombus sp.*	Japan
Kudo & Cooper	*Proceedings of the Royal Society B-Biological Sciences*	2019	*Bombus sp.*	Japan
Kudo	*Ecological Research*	2014	*Bombus sp.*	Japan
Martinez-Lopez et al.	*Global Change Biology*	2021	*Bombus sp.*	Mesoamerica: Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama
Soroye et al.	*Science*	2020	*Bombus sp.*	North America and Europe
Herrera	*Ecological Monographs*	2019	*Bombus sp.*	Spain
Franzen & Ockinger	*Journal of Insect Conservation*	2012	*Bombus sp.*	Sweden
Herbertsson et al.	*Basic and Applied Ecology*	2021	*B. terretris and B. lucorum*	Sweden
Ogilvie et al.	*Ecology Letters*	2017	*B. bifarius; B. flavifrons; B. appositus*	United States (USA)-Colorado
Richardson, et al.	*Journal of Insect Conservation*	2019	*Bombus sp.*	USA-Vermont
Tai et al.	*Journal of Insect Science*	2022	*Bombus sp.*	USA-Wisconsin
Mola et al.	*Journal of Animal Ecology*	2020	*B. vosesnesenskii*	USA-California
Smith et al.	*Environmental Entomology*	2016	*Bombus sp.*	USA-Missouri/Iowa
Mola & Williams	*Ecosphere*	2018	*Bombus sp.*	USA-California
Cole et al.	*Environmental Entomology*	2020	*Bombus sp.*	USA-California
Christman et al.	*Agriculture Ecosystems & Environment*	2022	*Bombus sp.*	USA-Utah
Pyke et al.	*Ecosphere*	2016	*Bombus sp.*	USA-Colorado
Ogilvie & CaraDonna	*Journal of Animal Ecology*	2022	*Bombus sp.*	USA-Colorado
Inouye	*Wiley Interdisciplinary Reviews-Climate Change*	2022	*Bombus sp.*	USA-Colorado

Appendix A2. Literature available for butterfly and climate studies.

Authors	Journal	Year	Focus taxa	Study location
Sbaraglia et al.	*Insect Conservation and Diversity*	2022	*Parnassius apollo*	Asia and Europe
Kearney et al.	*Biology Letters*	2010	*Heteronympha meropa*	Australia
Beaumont & Hughes	*Global Change Biology*	2002	Lepidoptera	Australia
Rodder et al.	*Scientific Reports*	2021	Lepidoptera	Austria
Herremans et al.	*Insects*	2021	*Aglais io*	Belgium
Pires et al.	*Anais da Academia Brasileira de Ciencias*	2020	Lepidoptera	Brazil
Matter et al.	*Insect Science*	2011	*Parnassius smintheus*	Canada
Bedford et al.	*Botany*	2012	Lepidoptera	Canada
Kharouba et al.	*Global Change Biology*	2014	Lepidoptera	Canada
Hellmann et al.	*Oecologia*	2008	*Erynnis propertius*; *Papilio zelicaon*	Canada
Wang et al.	*Ecosphere*	2016	Lepidoptera	China
Devictor et al.	*Nature Climate Change*	2012	Lepidoptera	Europe
Vermaat et al.	*Ambio*	2017	Lepidoptera	Europe
Hallfors et al.	*Ecology Letters*	2021	Lepidoptera	Finland
Corradini et al.	*Journal of Insect Conservation*	2021	*Limenitis populi*	France
Filz et al.	*European Journal of Entomology*	2013	Lepidoptera	Germany
Stuhldreher & Fartmann	*Ecological Indicators*	2018	*Erebia medusa*; *Satyrium spini*; *Melitaea aurelia*	Germany
Habel et al.	*Conservation Biology*	2016	Lepidoptera	Germany
Zografou et al.	*Plos One*	2014	Lepidoptera	Greece
Masy'ud et al.	*IOP Conference Series: Earth and Environmental Science*	2020	Lepidoptera	Indonesia
Tzachr et al.	*Israel Journal of Ecology & Evolution*	2008	Lepidoptera	Israel
Comay et al.	*Ecology and Evolution*	2021	Lepidoptera	Israel
Cerrato et al.	*Nature Conservation Bulgaria*	2019	Lepidoptera	Italy
Bonelli et al.	*Insects*	2022	Lepidoptera	Italy
Barve et al.	*Revista Mexicana de Biodiversidad*	2012	*Danaus plexippus*	Mexico
Molina-Martinez et al.	*Journal of Insect Conservation*	2013	Lepidoptera	Mexico
Molina-Martinez et al.	*Diversity and Distributions*	2016	Lepidoptera	Mexico
Hellegers et al.	*Frontiers in Ecology and Evolution*	2022	Lepidoptera	Netherlands
WallisDeVries et al.	*Oecologia*	2011	Lepidoptera	Netherlands

Authors	Journal	Year	Focus taxa	Study location
van der Kolk et al.	*Ecological Indicators*	2016	Lepidoptera	Netherlands
Crossley et al.	*Global Change Biology*	2021	Lepidoptera	North America
Colom et al.	*Proceedings of the Royal Society B-Biological Sciences*	2022	Lepidoptera	Northwest Mediterranean basin
Slancarova et al.	*Journal of Insect Conservation*	2015	Lepidoptera	Portugal
Topp et al.	*Diversity and Distributions*	2022	Lepidoptera	South Africa
Fitchett et al.	*International Journal of Biometeorology*	2022	*Belenois aurota*	South Africa
Kim & Kwon	*Journal of Asia-Pacific Biodiversity*	2018	Lepidoptera	South Korea
Kwon et al.	*Journal of Asia-Pacific Entomology*	2013	Lepidoptera	South Korea
Kwon et al.	*Zoological Studies*	2013	Lepidoptera	South Korea
Kwon et al.	*Environmental Entomology*	2010	Lepidoptera	South Korea
Lee et al.	*Sustainability*	2020	Lepidoptera	South Korea
Wilson et al.	*Ecology Letters*	2005	Lepidoptera	Spain
Gutierrez & Wilson	*Oecologia*	2014	*Gonepteryx rhamni*	Spain
Gordo & Sanz	*Ecological Entomology*	2006	*Pieris rapae*	Spain
Stewart et al.	*Ecology*	2020	Lepidoptera	Spain
Wilson et al.	*Global Change Biology*	2007	Lepidoptera	Spain
Stefanescu et al.	*Global Change Biology*	2003	Lepidoptera	Spain
Gil-Tapetado et al.	*Ecological Entomology*	2022	*Coenonympha pamphilus*	Spain and Portugal
Franzen & Ockinger	*Journal of Insect Conservation*	2012	Lepidoptera	Sweden
Karlsson	*International Journal of Biometeorology*	2014	Lepidoptera	Sweden
Johansson et al.	*Insect Conservation and Diversity*	2022	*Euphydryas aurinia*	Sweden
Altermatt	*Proceedings of the Royal Society B-Biological Sciences*	2010	Lepidoptera	Switzerland, France, and Germany
Ozdemirel	*Applied Ecology and Environmental Research*	2013	Lepidoptera	Turkey
Kaynas & Gurkan	*Entomological News*	2007	Lepidoptera	Turkey
Mair et al.	*Nature Climate change*	2014	Lepidoptera	United Kingdom (UK)
Isaac et al.	*Journal of Insect Conservation*	2011	Lepidoptera	UK
Carroll et al.	*Biological Conservation*	2009	*Aporia crataegi*; *Polyommatus semiargus*	UK
Bell et al.	*Diversity and Distributions*	2021	*Pyrgus malvae*	UK
Oliver et al.	*Nature Climate Change*	2015	Lepidoptera	UK

Authors	Journal	Year	Focus taxa	Study location
De Palma et al.	*Ecography*	2017	Lepidoptera	UK
Oliver et al.	*Ecography*	2013	*Aphantopus hyperantus*	UK
Warren et al.	*Nature*	2001	Lepidoptera	UK
Hill et al.	*Proceedings of the Royal Society B-Biological Sciences*	2002	Lepidoptera	UK
Pateman et al.	*Science*	2012	*Aricia agestis*	UK
Roy et al.	*Global Change Biology*	2015	Lepidoptera	UK
Wilson et al.	*Nature*	2004	Lepidoptera	UK
Hodgson et al.	*Global Change Biology*	2011	Lepidoptera	UK
Franco et al.	*Global Change Biology*	2006	*Coenonympha tullia; Aricia Artaxerxes; Erebia epiphron; Erebia aethiops*	UK
Roy & Sparks	*Global Change Biology*	2000	Lepidoptera	UK
Long et al.	*Journal of Animal Ecology*	2017	Lepidoptera	UK
Brooks et al.	*Ecography*	2017	Lepidoptera	UK
Roy et al.	*Journal of Animal Ecology*	2001	Lepidoptera	UK
Dennis & Sparks	*European Journal of Entomology*	2007	Lepidoptera	UK
Menendez et al.	*Proceedings of the Royal Society B-Biological Sciences*	2006	Lepidoptera	UK
Sparks & Yates	*Ecography*	1997	Lepidoptera	UK
Curtis & Isaac	*Journal of Insect Conservation*	2015	*Melitaea cinxia*	UK
Macgregor et al.	*Nature Communications*	2019	Lepidoptera	UK
Sparks et al.	*European Journal of Entomology*	2007	Lepidoptera	UK
Stalhandske et al.	*Journal of Animal Ecology*	2017	Lepidoptera	UK and Sweden
Wells & Tonkyn	*Insect Conservation and Diversity*	2014	*Speyeria diana*	US- east coast
Nice et al.	*Ecology*	2014	Lepidoptera	USA- California
Matter & Roland	*Ecosphere*	2015	*Parnassius smintheus*	USA- Colorado
Thorne et al.	*Ecological Applications*	2006	Lepidoptera	USA- California
Wepprich et al.	*Plos One*	2019	Lepidoptera	USA- Ohio
Forister et al.	*Science*	2021	Lepidoptera	USA- western states
Nelson et al.	*Journal of the Lepidopterist's Society*	2020	Lepidoptera	USA- Colorado
Swengel & Swengel	*Journal of Insect Conservation*	2007	*Callophrys irus; Speyeria idalia; Lycaeides melissa samuelis*	USA- Wisconsin
Vogel et al.	*Biological Conservation*	2007	Lepidoptera	USA- Iowa

Authors	Journal	Year	Focus taxa	Study location
Swengel et al.	*Journal of Insect Conservation*	2011	*Callophrys irus; Speyeria idalia; Lycaeides melissa samuelis*	USA- Wisconsin, Iowa, Minnesota, Illinois
Vogel et al.	*Journal of Insect Conservation*	2010	Lepidoptera	USA- Iowa
Henderson et al.	*Biological Conservation*	2018	*Speyeria idalia*	USA- Wisconsin
Swengel	*Biological Conservation*	1996	*Callophrys irus; Speyeria idalia; Lycaeides melissa samuelis*	USA- Illinois, Iowa, Minnesota, Missouri, Wisconsin
Huntzinger	*Biological Conservation*	2003	Lepidoptera	USA- California, Oregon
Pavlik et al.	*Natural Areas Journal*	2017	Lepidoptera	USA- California
Swengel & Swengel	*Journal of Insect Conservation*	2015	Hesperiidae	USA- Wisconsin
Dartnell et al.	*Journal of Insect Conservation*	2022	Lepidoptera	USA- California
Fleishman	*Environmental Management*	2000	Lepidoptera	USA- Nevada
McIver & Macke	*Rangeland Ecology & Management*	2014	Lepidoptera	USA- western states
Larsen et al.	*Scientific Reports*	2022	Lepidoptera	USA- northeast states
Woods et al.	*Environmental Entomology*	2008	Lepidoptera	USA-Ohio
McLaughlin et al.	*Proceedings of the National Academy of Sciences of the United States of America*	2002	*Euphydryas editha bayensis*	USA-California
Forister et al.	*Proceedings of the National Academy of Sciences of the United States of America*	2010	Lepidoptera	USA- California
Forister et al.	*Journal of Insect Science*	2011	*Glaucopsyche lygdamus*	USA-California
Halsch et al.	*Ecological Entomology*	2020	*Agraulis vanillae*	USA-California
Zipkin et al.	*Global Change Biology*	2012	*Danaus plexippus*	USA-Ohio, Texas
Kucherov et al.	*Plos One*	2021	Lepidoptera	USA- Illinois
Zipf et al.	*International Journal of Biometeorology*	2017	Lepidoptera	USA-Massachusetts
Forister & Shapiro	*Global Change Biology*	2003	Lepidoptera	USA-California
Casner et al.	*Conservation Biology*	2014	Lepidoptera	USA-California
Pardikes et al.	*Ecology*	2015	Lepidoptera	USA-California
Williams et al.	*Journal of the Lepidopterist's Society*	2014	Lycaenidae	USA-Massachusetts
Gezon et al.	*Insects*	2018	Lepidoptera	USA-Florida
Geest & Baum	*Environmental Entomology*	2021	*Speyeria sp.*	USA- eastern states
Zylstra et al.	*Global Change Biology*	2022	*Danaus plexippus*	USA/Mexico

APPENDIX B

Appendix B1. Database Overview by classification (federal, university, public/state, citizen science, mixed, and private collections) for each taxonomic group. Numbers represent data downloads from online sources as of September 15, 2022; other records observed in-person are denoted as such within the database type. Repositories may continue to digitize records relevant to this study after this date based on taxonomic requests, personnel support, and funding.

Database Type	*Bombus*	Hesperiidae	Lycaenidae	Nymphalidae	Papilionidae	Pieridae	Total
Citizen science (online/field collection)	800	87	319	914	146	122	2388
Federal Repository (online and in-person)	879	0	2243	190	1273	1	4586
Mixed (online)	626	67	325	191	25	57	1291
Private Resource (in-person)	0	25	1	10	1	0	37
State Repository (online)	6	9	0	27	3	0	45
University (online and in-person)	1210	68	125	368	18	15	1704
Total	3521	256	3013	1600	1466	195	10051

Appendix B2. Database Overview by classification (federal, university, public/state, citizen science, mixed, and private collections). Numbers represent data queries as of September 15, 2022. Repositories may continue to digitize records relevant to this study after this date based on taxonomic requests, personnel support, and funding. *GBIF and SCAN data repositories store similar records and cross-reference each other through their metadata. For this analysis specific to the GYE, the repositories storing data through GBIF/SCAN were pulled through these database repositories rather than from the specific institution. #Records from C.P. Gillette Museum of Arthropod Diversity were both studied in-person and virtually to validate SCAN/GBIF digitization efforts. %Records are also stored within iDigBio with some cross-reference amongst datasets, which accounts for data overlaps that were filtered in the analysis.

Database	Collection Type	Total # Records Digitized/ Available	Total #/% Records with Images	Total % Records Missing Species-Level ID	Total % Records Missing Locational Attributes	Total % Records Missing Temporal Attributes	Total # Records Digitized-GYE
*Academy of Natural Sciences Entomology Collection – LepNet (ANSP-ENT)	Federal	49,782	1,787 (4%)	14%	79%	<0.01%	21
*American Museum of Natural History (AMNH)	Federal	370,171	Unknown	8%	1%	<0.01%	434
*Arizona State University	University	164,802	5,918 (4%)	14%	0%	<0.01%	1
BISON-BugGuide	University	527,659	Unknown	3%	14%	0%	88
*C.A. Triplehorn Insect Collection at the Ohio State University	University	541,961	997 (0.18%)	66%	0%	13%	171
*Chicago Academy of Sciences (CHAS)	University	26,186	3 (0.01%)	50%	61%	0%	1
*%Cleveland Museum of Natural History (CLEV)	State	126,703	9 (0.01%)	51%	3%	0%	55

Database	Collection Type	Total # Records Digitized/ Available	Total #/% Records with Images	Total % Records Missing Species-Level ID	Total % Records Missing Locational Attributes	Total % Records Missing Temporal Attributes	Total # Records Digitized-GYE
*#C.P. Gillette Museum of Arthropod Diversity at Colorado State University (CSU)	University	278,069	14,841 (5%)	5%	7%	2%	1264
*Denver Museum of Nature and Science (DMNS)	State	119,718	2,643 (2%)	65%	3%	2%	34
*Essig Museum of Entomology (EMEC)	University	318,994	1 (0%)	88%	7%	2%	129
*Field Museum of Natural History (FMNH)	Federal	476,881	18,231 (4%)	98%	27%	15%	52
*%University of Georgia (GMNH)	University	28,779	10 (0.03%)	17%	5%	1%	20
Yellowstone Heritage and Research Center (HRC)	Federal	263	0	0%	56%	11%	263
Harp Collections	Private	30	0	0%	100%	100%	30
%iDigBio	Mixed	67,253,377	4,884,794 (4%)	Unknown	Unknown	Unknown	2867
*iNaturalist	Citizen science	6,923,143	5,537,744 (93%)	10%	0%	0%	2388
*Illinois Natural History Museum (INHS)	University	1,078,785	Unknown	44%	42%	12%	16
*%University of Kansas (KU)	University	1,374,142	422,931 (31%)	79%	26%	<0.01%	18
*Natural History Museum of Los Angeles County	State	605,573	Unknown	79%	28%	16%	15

Database	Collection Type	Total # Records Digitized/ Available	Total #/% Records with Images	Total % Records Missing Species-Level ID	Total % Records Missing Locational Attributes	Total % Records Missing Temporal Attributes	Total # Records Digitized-GYE
Lepidopterist's Society (LEPSOC)	Mixed	124,592	Unknown	3%	22%	<0.01%	152
*Museum of Comparative Zoology, Harvard University (MCZ)	University	709,577	127,573 (18%)	98%	18%	31%	88
*Museum of Northern Arizona (MNA)	University	116,687	1,235 (1%)	61%	3%	<0.01%	4
*Milwaukee Public Museum (MPM)	State	48,477	1,180 (2%)	3%	96%	39%	9
*Albert J. Cook Arthropod Research Collection (MSU)	University	312,088	12,942 (4%)	29%	40%	37%	106
*University of Central Florida (UCFC)	University	564,020	1 (0%)	84%	0%	<0.01%	4
*%University of New Mexico (UNM)	University	59,236	75 (0.13%)	50%	0%	2%	10
*University of Alberta (UASM)	University	342,167	Unknown	19%	0%	<0.01%	10
*University of Texas Insect Collection (UTIC)	University	38,465	526 (1%)	25%	3%	<0.01%	1
*%Oregon State Arthropod Collection (OSAC)	University	96,710	106 (1%)	41%	65%	<0.01%	7
*%Santa Barbara Museum of Natural History (SBMNH)	State	116,651	1,452 (1%)	51%	0%	<0.01%	1

Database	Collection Type	Total # Records Digitized/ Available	Total #/% Records with Images	Total % Records Missing Species-Level ID	Total % Records Missing Locational Attributes	Total % Records Missing Temporal Attributes	Total # Records Digitized-GYE
*%Texas A&M University (TAMU)	University	1,046,105	Unknown	31%	10%	5%	3
*%University of California Davis R.M. Bohart Museum of Entomology (UCD)	University	120,647	291 (0.24%)	60%	82%	37%	11
*University of Michigan Museum of Zoology (UMMZ)	University	386,629	Unknown	99.6%	9%	<0.01%	2
*%University of Colorado Museum of Natural History	University	100,743	584 (0.58%)	14%	0%	44%	1
*University of California Riverside (UCRC)	University	181,026	Unknown	19%	6%	Unknown	19
*%Natural History Museum of Utah (UMNH)	University	78,331	4,353 (6%)	49%	3%	8%	138
*University of Minnesota (MIN)	University	294,681	Unknown	82%	26%	8%	45
*USDA-ARS: Bee Biology and Systematics Lab	Federal	629,545	Unknown	1%	2%	52%	1523
*University of Wyoming Dillon Lab Insect Collection (UWYMED)	University	16,476	Unknown	98%	1%	<0.01%	12

Database	Collection Type	Total # Records Digitized/ Available	Total #/% Records with Images	Total % Records Missing Species-Level ID	Total % Records Missing Locational Attributes	Total % Records Missing Temporal Attributes	Total # Records Digitized-GYE
*Virginia Polytechnic Institute and State University (VPI)	University	15,622	6,771 (45%)	32%	7%	5%	23
*%Western Washington University (WWU)	University	4,039	2,173 (54%)	10%	17%	22%	3
*William F. Barr Entomological Museum (UI-WFBM)	University	55,743	2,057 (4%)	7%	11%	3%	26
Yale Peabody Museum (YPM)	University	385,554	372,860 (97%)	99%	4%	Unknown	1001
*Smithsonian Institution (SI-NMNH)	Federal	712,629	Unknown	43%	68%	Unknown	26
*Bombus of Canada	University	16,088	Unknown	0%	2%	Unknown	11
Yellowstone 4th of July Butterfly Count	Private	47	0	0	0	0	47
NPS Research Permit and Reporting System (RPRS)	Federal	NA – database that stores permit and annual reports	NA	NA	NA	NA	4483

Appendix C1. Table representing field site metadata across the GYE.

Park	Location	Habitat	Elevation (m)	Sampling Years	Visits	Observers	Observations	Sampling Time (minutes)
GRTE	Death Canyon	Meadow	2101	2017-21	16	6	534	2824
	Granite Canyon	Meadow	1988	2019-21	9	6	650	1701
	Taggart Lake	Meadow	2105	2019	1	6	41	126
	Bradley Lake	Meadow	2152	2019	1	6	46	90
	Ditch Creek	Sagebrush	2059	2021	3	6	156	251
	Two Oceans	Meadow	2158	2020-21	9	6	507	1189
	Pacific Creek	Meadow	2116	2020-21	3	6	98	240
YELL	Lamar Valley	Meadow	2091	2017-19; 21	18	4	547	1732
	Bunsen Peak	Sagebrush	2335	2017-19; 21	18	4	360	1492
	Tower Junction	Sagebrush	1906	2017-19	6	4	116	637
	Mammoth	Sagebrush	1828	2017-19	4	4	36	419
	Washburn Top	Subalpine	2790	2017-19; 21	7	4	179	537
	Washburn North	Subalpine	2653	2017-19; 21	7	4	161	283
	Dunraven	Meadow	2692	2017-19; 21	7	5	98	578
	Cougar Creek	Meadow	2102	2017-21	20	6	1051	3108
GYE Sites	Fantan Lake	Subalpine	2944	2020	1	5	0	123
	Beartooth Pass	Subalpine	3215	2020	1	5	22	266
	Line Creek Plateau	Subalpine	3029	2020	1	5	54	364
	Teepee Creek	Sagebrush	1789	2020	1	5	103	294
	Christmas Lake	Subalpine	3158	2020	1	5	4	60
	Porcupine Creek	Meadow	1973	2020	1	5	99	65
Totals	21 sites				135	5	4,862	16,379

Appendix C2. List of floral and plant species tracked by NPN/NEON sites and CSU field collections, and the seasonality stage present in the GYE as defined by Bloom et al. (2022).

Scientific Name	Seasonality	Scientific Name	Seasonality
Prunus virginiana	Berries	*Achillea millefolium*	Mid-summer
Symphoricarpos albus	Berries	*Geranium viscosissimum*	Mid-summer
Mahonia repens	Berries	*Phlox longifolia*	Mid-summer
Amelanchier alnifolia	Berries	*Senecio integerrimus*	Mid-summer
Rosa woodsii	Berries	*Arnica cordifolia*	Mid-summer
Shepherida canadensis	Berries	*Maianthemum racemosa*	Mid-summer
Lonicera utahensis	Berries	*Maianthemum stellatum*	Mid-summer
Balsamorhiza sagittata	Early spring	*Lupinus sericeus*	Mid-summer
Artemisia tridentata	Early spring	*Fritillaria atropurpurea*	Mid-summer
Claytonia lanceolata	Early spring	*Frasera speciosa*	Mid-summer
Ranunculus glaberrimus	Early spring	*Wyethia amplexicaulis*	Mid-summer
Ipomopsis aggregata	Early spring	*Lupinus argenteus*	Mid-summer
Eriogonum umbellatum	Early spring	*Potentilla gracillis*	Mid-summer
Orogenia linearifolia	Early spring	*Gilia aggregata*	Mid-summer
Fritillaria pudica	Early spring	*Linum lewsii*	Mid-summer
Viola nuttallii	Early spring	*Sedum stenopetalum*	Mid-summer
Dodecatheon pulchellum	Early spring	*Crepis acuminata*	Mid-summer
Lithophragma parviflorum	Early spring	*Corallorhiza striata*	Mid-summer
Phlox hoodii	Early spring	*Eremogone congesta*	Mid-summer
Hydrophyllum capitatum	Early spring	*Helianthella uniflora*	Mid-summer
Disporum trachycarpum	Early spring	*Cirsium arvense*	Non-native
Geum triflorum	Early spring	*Bromus tectorum*	Non-native
Delphinium nelsonii	Early spring	*Taraxacum officinale*	Non-native
Clematis hirsutissima	Early spring	*Carduus nutans*	Non-native
Lithospermum ruderale	Early spring	*Centaurea stoebe*	Non-native
Viola adunca	Early spring	*Tragopogon dubius*	Non-native
Chamerion angustifolium	Late summer		
Perideridia gairdneri	Late summer		
Galium boreale	Late summer		
Campanula rotundifolia	Late summer		
Calochortus nuttallii	Late summer		

LIST OF ABBREVIATIONS

AOA – Areas of Analysis

ESA – Endangered Species Act

GBIF – Global Biodiversity Information Facility

GRTE – Grand Teton National Park

GYE – Greater Yellowstone Ecosystem

IPBES – Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services

IPCC – Intergovernmental Panel on Climate Change

NEON – National Ecological Observatory Network

NHCs – Natural History Collections

NOAA – National Oceanic and Atmospheric Association

NPN – National Phenology Network

NPS – National Park Service

NRCS – Natural Resources Conservation Service

PCA – Principal Component Analysis

PC – Principal Component

RCP – Representative Concentration Pathway

SCAN – Symbiota Collection of Arthropods Network

US – United States

YELL – Yellowstone National Park