PLOS ONE

Bee and butterfly records indicate diversity losses in western and southern North America, but extensive knowledge gaps remain

Sara K. Souther[1], Manette E. Sandor[2,3], Martha Sample[1], Sara Gabrielson[4], Clare E. Aslan[1] *

1 Center for Adaptable Western Landscapes, Northern Arizona University, Flagstaff, AZ, United States of America, 2 Department of Ecology, Evolution, and Environmental Biology, Columbia University, New York, NY, United States of America, 3 Center for Conservation and Biodiversity, American Museum of Natural History, New York, NY, United States of America, 4 Department of Biology, Northern Arizona University, Flagstaff, AZ, United States of America

* clare.aslan@nau.edu

Abstract

Pollinator losses threaten ecosystems and food security, diminishing gene flow and reproductive output for ecological communities and impacting ecosystem services broadly. For four focal families of bees and butterflies, we constructed over 1400 ensemble species distribution models over two time periods for North America. Models indicated disproportionally increased richness in eastern North America over time, with decreases in richness over time in the western US and southern Mexico. To further pinpoint geographic areas of vulnerability, we mapped records of potential pollinator species of conservation concern and found high concentrations of detections in the Great Lakes region, US East Coast, and southern Canada. Finally, we estimated asymptotic diversity indices for genera known to include species that visit flowers and may carry pollen for ecoregions across two time periods. Patterns of generic diversity through time mirrored those of species-level analyses, again indicating a decline in pollinators in the western U.S. Increases in generic diversity were observed in cooler and wetter ecoregions. Overall, changes in pollinator diversity appear to reflect changes in climate, though other factors such as land use change may also explain regional shifts. While statistical methods were employed to account for unequal sampling effort across regions and time, improved monitoring efforts with rigorous sampling designs would provide a deeper understanding of pollinator communities and their responses to ongoing environmental change.

Introduction

Over 85% of global flowering plants, including a third of crop species, are pollinated by animals [1], but declining pollinator populations have been detected in systems worldwide [2–4].

Pollinator declines have been traced to a suite of drivers including biological invasions, disease and parasites, habitat loss, pesticides, monocropping, and climate change [5, 6]. However, reports of declines are typically limited to well-studied taxa, agricultural areas, locations near human communities, and other systems that are easy to access and study [e.g., 7–10]. We lack a comprehensive understanding of which species contribute effectively to pollination or their population dynamics and distributions. Most pollinators are cryptic, and data collection is often limited to circumstances in which observers have access to sufficient training, technologies, sample preservation, and/or record-keeping [11, 12].

Pollinator losses have caused alarm among scientists and policymakers alike because they impact ecological systems at a foundational level [13–15]. Gene flow among plants maximizes their genetic diversity and thus both reproductive output and adaptability in the face of ongoing environmental change [16–18]. Although many plants are capable of self-fertilization or abiotic pollination, most plant species are at least partially dependent on pollinating animals including insects, birds, mammals, and reptiles [1]. Decreased seed output affects the distribution and relative abundance of plants in ecological communities and has the potential to reduce ecosystem resilience following disturbance [19–21]. In terrestrial systems, plants are foundational to all ecosystem services, since they mediate the supporting services (soil formation, photosynthesis, primary production, nutrient cycling, and water cycling) that underlie provisioning, regulating, and cultural services [22].

A broader understanding of geographic trends in pollinator diversity and declines can support conservation and restoration planning as well as public education promoting pollinator-friendly practices and sustainability [23]. Such information can also spur continued ecological research and monitoring of areas with particularly high recorded pollinator diversity, which may act as critical pollinator hotspots, as well as areas that are likely undersampled [24–26]. To facilitate these activities, we set out to assess the current state of knowledge of pollinators of North America (Canada, the United States, and Mexico), examining spatial and temporal trends in presence records of key pollinator families, known and potential pollinator genera, and relatively well-studied pollinator species of concern.

This study consisted of three parts: (1) First, we assessed evidence of spatial patterns over time for four well-known pollinator families: Apidae, Megachilidae, Pieridae, and Papilionidae. We developed species distribution models for North America to assess areas of diversity and change for these families. (2) To further explore spatial patterns of likely pollinator vulnerability with a group for which we have greater taxonomic resolution and greater monitoring focus, we mapped records of species of conservation concern that are known flower visitors and may therefore transfer pollen. (3) We mapped spatial records of a broad set of genera containing flower visitors that have been recorded feeding on pollen, nectar, or flowers and transporting pollen. This provided us with a coarse overview of the state of knowledge of potential pollen-carriers in North America. Our results highlight areas of pollinator vulnerability as well as key knowledge gaps, helping to advance the scientific and management dialogue surrounding pollinator conservation.

Materials and methods

Data extraction from GBIF

For all three components of the study, we extracted occurrence records of known and potential pollinators from the Global Biodiversity Information Facility, an international repository for species occurrence data (GBIF.org (2020), GBIF Home Page. Available from: https://www.gbif.org [2 March 2020]). GBIF amalgamates nearly two billion species occurrence records from museum collections to geolocated community science records [27], and as such is an invaluable resource for information on understudied species with little or no representation in

the published literature. We queried GBIF at the species level for all North American records of Apidae, Megachilidae, Pieridae, and Papilionidae, as well as for records of all species of conservation concern.

Part 1: Patterns of spatial and temporal diversity: Apidae, Megachilidae, Pieridae, and Papilionidae

We selected the bee families Apidae and Megachilidae and the butterfly families Pieridae and Papilionidae for spatial analysis because they are relatively well-known and of interest to researchers, with life history traits better described than is the case for many other invertebrate pollinator families. Apidae is the largest family of bees in the world and includes bees important to agriculture (e.g., *Apis mellifera* and *Bombus impatiens*) as well as large numbers of lesser-known bees [28]. A wide diversity of bee life history traits is represented within the Apidae, including both eusociality and solitary habits, ground nesting, stem nesting, and wood nesting, and cleptoparasitism [28], and many Apidae collect pollen on their legs. Megachilidae are mostly above-ground cavity nesters and collect pollen on their abdomens. Because they span a range of resource and foraging requirements, the two families of bees together may act as a proxy for lesser-known groups that require pollen, range in morphology and feeding behavior, and utilize a diversity of nesting resources. The two focal butterfly groups include many charismatic species that are readily identified on the wing (e.g., for Pieridae, the whites and sulfurs; for Papilionidae, the swallowtails), and the two families span wide elevational ranges and wide taxonomic variation in host plant families [29–31], again suggesting that patterns of diversity among these groups may be reliable indicators of broader patterns among less-studied pollinators with overlapping and diverse requirements.

For these four families, we extracted all GBIF records over North America at the species level. We used a records extraction code developed using R version 3.6.2 (R Core Development Team 2016) to extract occurrences of pollinator taxa from GBIF. We queried the GBIF database using the R-package 'rgbif' with standard data cleaning protocols (r-package = 'CoordinateCleaner') [32]. The code extracted from GBIF the spatial distribution, number of observations, time of each observation, and mode of detection. Although observation number is not a direct measure of abundance since it is biased by detectability, observer effort, and accessibility of sites, low or declining rates of occurrence in the detection database could highlight taxonomic groups that warrant further investigation, and frequency of observation can be used to compare and contrast the state of knowledge of pollinators across regions, time periods, and mode of detection. To summarize outputs by ecoregion and examine patterns of detections over space, we used georeferenced data points from the Ecoregions of North America Level 1 [33, 34], as well as from the North American Land Change Monitoring System Landsat 30m data layers. The use of ecoregions, which are defined as areas containing generally consistent ecosystem type and environmental resources [34], maximizes the potential policy and conservation relevance of our analyses, by linking findings to areas where management needs and strategies may be generally consistent [34].

We used species distribution models (SDMs) to determine the species ranges of 923 species of pollinators within the four families. We analyzed the occurrence records of these species over Canada, the US, and Mexico. We spatially thinned all occurrence records at the species level using a randomization algorithm (*R-package 'spThin'*) to a minimum of 10 km distance between individual observations. We retained only those species which had 10 or more occurrence records for analysis.

We pulled all 19 bioclimatic variables from WorldClim with a grid resolution of 2.5 minutes [35]. We used WorldClim data because it is available for all of North America, including

Mexico, unlike many other sources of climate data, and (2) because for the time period comparison analysis described below we required historical climate data. We chose this low grid resolution because our analyses were continental in extent, and we were looking for broad patterns across multiple species. To accurately model the environment-occurrence relationships of each species, we reduced the geographic extent of the environmental input data to a box encompassing all occurrence points for any given species [36, 37]. We designated boundaries of this box by rounding the maximum latitude and longitude across all observations up to the nearest whole number and rounding the minimum down to the nearest whole number. For each species, we calculated the variance inflation factor between each of the climate variables and every other climate variable. Highly correlated variables were excluded in a stepwise fashion (R package 'usdm'; R Core Team 2020) [38].

We ran SDMs in an ensemble model framework (R package 'sdm' 2016; R Core Team 2020) [39], which accounts for the uncertainty due to different modeling approaches [40–42], consisting of the following modeling approaches: general linear model ('glm'), general additive model ('gam'), flexible discriminant analysis ('fda'), and multivariate adaptive regression spline ('mars'). Each species model used 10,000 randomly-selected background points, with the exception of nine species that had too small of a geographic distribution to support this many background points, for which the highest number possible, rounded to the nearest 1000, was used [37]. Each species model was subjected to cross validation [43], whereby the data were randomly split into five roughly equal groups, and in each of the five times the model was fit, one group was used as test data and the other four groups were used as training data such that each of the five groups were used as test data for one of the model fits [39]. We ran three iterations of each of five cross-validation sets, resulting in a total of 60 models across the four model methods. We built weighted average ensemble models for each species where the weighted average was calculated based on the cross-validation performance of the model, using the true skill statistic (TSS) as a threshold [39, 44]. We projected the probability of presence for each species back onto North America but limited by the original bounding box to avoid locations of predicted presence where appropriate climatic conditions were identified by the model but no known occurrences exist. We then converted the continuous probability of presence to binary ('present' or 'absent'), using TSS as the threshold [45]. After thresholding, we summed all species either within or across all of Papilionidae, Apidae, Megachilidae, and Pieridae to create species richness maps.

GBIF records the 'basis of origin' of each observation when possible; these categories include: *fossil specimens*, *living specimens*, *machine observations* (an observation made by a machine), *material citation* (observation cited in a publication), *preserved specimen* (observation from a herbarium or museum), *human observations* (an observation made by one or more people; almost all digital), and a catch-all of simply *occurrence*, when origin is not established. For all occurrences of known origin, we separate human observation (digital) from all other observations to look at differences through time in collection types and thus separate effects of data collection method from true patterns of occurrence.

To assess change in diversity and distribution over time, we split our data into two time periods: 1939–1979 and 1980–2020. This resulted in two datasets (S3 Table) and had two advantages: (1) the more recent time period contains almost all of the digital records, so is a different type of data; and (2) rapid increases in average temperatures have been recorded in North America since 1980, such that abiotic conditions across the continent are different between the two time periods. Because of this abrupt shift in methodologies and climate aligning to the time periods, changes in richness or distribution of taxa between the time periods may be driven by either altered detection or altered climate context, whereas patterns observed within a given time period are less likely to be artifacts of either of these influences but may

instead be due, for example, to other forms of environmental change. From the 1980's to the present, each decade was hotter than the last [46], giving the 1980–2020 time period a more pronounced signature of climate change that we could compare to a historical period with less climate change impact. (We recognize that climate change may not be the only driver of species' range shifts within pollinators. While land use change may be the largest driver of pollinator range shifts, historical data for Mexico is not available to the same degree as for the U.S. and Canada. The countries exhibit differences in land use change and policies (for example, DDT was banned in the U.S. and Canada in 1972 [47] with some use continuing in Canada until 1990 [48] and use in Mexico persisted until 2000 [49]) but data availability and such factors co-vary and are difficult to separate.) Because some species were not recorded in one of the two time periods, these species were discarded. We were left with 736 species across the four families (79.7% of the total) for use in our time-period comparisons.

We pulled climate data by decade from WorldClim version 1 on 12/23/2021, beginning with the earliest decade available, the 1960s. Thus, climate data for the pollinator records from 1939–1979 was compiled from 1961–1979. Climate data for the pollinator records from 1980–2020 spanned the period 1980–2018 because 2018 was the last available year of data. Thus, although the two time periods therefore contained equal numbers of years, the lack of availability of climatic data prior to 1960 resulted in the first time period being trained on the latter 18 years of climate data within the period—a factor that makes our analysis more conservative by potentially diminishing the average climatic differences between the time periods. Across all locations within our dataset, the annual mean temperature for 1980–2020 minus that from 1939–1979 ranged from a minimum of 0 to a maximum of 1.6 (mean = 0.8) degrees C. Mean annual precipitation calculated in the same way ranged from -848 to 400 (mean = 7.19) mm. We created monthly averages for minimum temperature, maximum temperature, and precipitation across each of the two time periods, and cropped each of these to North America. We then created BioClim variables for our two time periods ("biovars" function within the R package 'dismo'; R Core Team 2020) [50].

We ran SDMs in an ensemble model framework as described above. We created one set of ensemble models for the first time period and one for the second time period. To determine how the predicted ranges of species differed between 1939–1979 and 1980–2020, after thresholding we determined the percentage of area predicted for 1980–2020 as compared to 1939–1979 [51, 52]. We additionally calculated the difference between the predicted range, after thresholding, for each species for 1980–2020 and for 1939–1979. This measure of change determines where species are predicted to have expanded into new areas and where species have been lost from an area in 1980–2020 as compared to 1939–1979.

We transformed the thresholded presence-absence species distribution rasters into shapefiles and calculated the distance and direction of movement of the centroid of the species' range. We determined the centroid of the range and distance moved from the first to the second time period (R package 'geosphere'; R Core Team 2020) [53]. We used Haversine distance calculations to get distance output in meters.

Part 2: Patterns of vulnerability: Species of concern

The SDMs described above were compiled across families, but the lack of resolution in much of GBIF makes it difficult to relate patterns to individual species or to examine potential causes of vulnerability. We addressed this limitation in two ways: (a) we mapped occurrence records for North American pollinator species of concern, which have been relatively well-studied due to their known rarity and relevance to management and policy; and (b) we included vertebrate pollinators, for which species-level records are more reliable, in both parts 2 and 3 of this

study. We constructed a list of the species of conservation concern across the three countries in order to analyze spatial occurrence of such species and identify regions of vulnerability. We used the International Union for the Conservation of Nature (IUCN) Red List, version 3, to extract conservation status for all nectivorous vertebrates in the database. The IUCN Red List uses expert consensus to assess species worldwide and assign them to threat-level categories including Extinct, Extinct in the Wild, Critically Endangered, Endangered, Vulnerable, Near Threatened, Least Concern, and Data Deficient. Assessments indicate the quantity of population decline or range contraction that has been observed for a particular species or is deemed likely based on current threats to that species. The IUCN Red List provided an initial list of 11 vertebrate pollinators of conservation concern for North America (S2 Table). Although the IUCN Red List is far less developed for invertebrates than for vertebrates, we also downloaded from the Red List webpage the IUCN conservation status of all invertebrates that may interact with flowers for any of the three focal countries. Twenty-five of these invertebrates (37%) were rated as Near Threatened or in worse status on the Red List. We additionally examined national and state/province-level conservation assessments to seek other potential pollinator species of conservation concern. At the national level, these assessments included listings by Canada's Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (https://www.canada.ca/en/environment-climate-change/services/species-risk-public-registry.html), the US Endangered Species Act (16 U.S.C. 1531–1544) and the Mexican Official Norm NOM-059-SEMARNAT-2010 (*Protección ambiental-Especies nativas de México de flora y fauna silvestres*). At the state or province level, these assessments included Canadian province listings (obtained by examining each provincial government website), US state listings (obtained by examining each state government website as well as, when those websites referred to them in their listings, State Wildlife Action Plans), and Mexico's *Estrategias Estatales de Biodiversidad* (https://www.biodiversidad.gob.mx/region/EEB/estrategias.html). Once we had used these lists to develop a database of species of conservation concern that are known or likely to feed on pollen, nectar, or flowers, we applied our GBIF query code at the species level to each species of concern in turn to obtain its observation number and frequency, spatial distribution, and ecoregion. We then fed all outputs into our database to summarize occurrence of threatened species spatially and taxonomically. These overviews allowed us to compare species-level patterns with the less-resolved family and genus-level patterns provided in parts 1 and 3 of the study, enabling validation and biological interpretation. Relating patterns of decline, vulnerability, and richness to known distributions of species of concern allow us to consider the implications of such patterns for conservation and monitoring.

There are 1159 species of concern listed in international (59 species), national (35 species), or state/provincial sources (1065 species). Vertebrates of concern include four bats and seven hummingbirds, all ranked as Near Threatened, Vulnerable, Endangered, or Critically Endangered by the IUCN (S2 Table). Among invertebrates, 4.3% of species of concern are Diptera, 3.9% are Coleoptera, 13.4% are Hymenoptera, and 78.4% are Lepidoptera. Here a likely knowledge gap emerges: Lepidoptera are more easily detected and identified in the field than the other insect groups, and it is likely that records of their occurrence and decline are therefore more complete [54].

Part 3: Diversity assessment of potential pollinator occurrence across North America

To explore geographic and temporal patterns of potential pollinator occurrence, we used existing studies of pollination and lists of pollinators in North America to assemble a full genus list of potential pollen carrying taxa with which to query GBIF using the code above. We

deliberately took a broad, umbrella approach to this analysis. Pollination is messy, with most plants producing large numbers of pollen grains and most pollen lost to the environment [55–57]; even plants that exhibit evidence of pollination syndromes and likely have a single or small number of high-efficiency pollinators are often found to receive pollen from other flower-visiting taxa as well [58]. Likewise, some flower visitors transfer extremely small number of pollen grains in an incidental fashion yet contribute measurably to plant reproduction, whereas others (especially bees) transfer thousands of pollen grains directly between plant individuals [59, 60]. To account for the diffuse nature of pollination networks and the possibility that many taxa provide functional redundancy within systems, we included in our search all genera known to contain taxa that have been recorded as carrying pollen [61]; in addition to nectarivores, palynivores, and florivores, such genera also include omnivores and other opportunistic visitors that pick up pollen in the course of their foraging. Knowledge gaps assessed through this process thus indicate areas of undersampling of the community of potential pollinators in the broadest sense.

To assemble this list of genera, we used overviews and databases of pollination, pollinators, and pollen-carrying taxa in North America, including Discover Life (https://www.discoverlife.org/), the Biosystematic Database of World Diptera (https://www.gbif.org/dataset/f49035c5-335a-418f-bafb-24e0ce03cb27), and BugGuide (https://bugguide.net/node/view/15740, and published sources [62–115] (S1 Table). Although taxonomy among invertebrates is often poorly resolved and genera can be frequently redefined, we nevertheless select genus level for this extraction for several key reasons. We aim to capture as much as possible the full diversity of potential flower visitors, yet only a small fraction of invertebrate species beyond the bees and butterflies have been examined for diet or pollen transport, so a species-level analysis would be too restricted in scope. Family, by contrast, is far too coarse to assume similar form and function within a taxonomic group. Many potential pollinators are difficult to identify to species without advanced taxonomic skill and technology, and genus-level records in many cases are therefore likely more reliable than species-level. There is also large variation in nomenclature applied to samples in GBIF, particularly when samples span many decades of collection date, and use of genus instead of species accounts for many synonyms [23]. This component of our study aims to take a broad, umbrella approach to identify key knowledge gaps, which mitigates the imprecision that accompanies the use of genera for invertebrates since our key take-home messages center on where detections are most prevalent and which areas seem under-sampled.

To include vertebrate pollinators in North America, we included the list of known pollen-carriers provided in Aslan et al. [62], which includes 228 vertebrates including icterids, picids, tanagers, hummingbirds, and nectar-feeding bats. Among bird pollinators, major families include Icteridae (23 species), Cardinalidae (9 species), Thraupidae (13 species), Fringillidae (11 species), Parulidae (9 species), and Trochilidae (109 species). Mammalian pollinators include 16 species of nectarivorous bats (Phyllostomidae). For each of these vertebrate species, we used the query code described above to extract from GBIF observation number and frequency, spatial distribution, observation time horizon, and ecoregion for the full list of vertebrates.

To quantify generic diversity of potential pollen-carrying taxa across ecoregions, we calculated incidence-based Hill numbers in R (version 3.6.3.) package *'iNext'*. Hill numbers follow a doubling property; that is, if you combine two equally large and diverse assemblages that share no taxa, the resulting assemblage will be twice as diverse as the individual assemblages, allowing meaningful comparisons across data types, including taxonomic, phylogenetic and functional diversity data [116, 117]. Generic richness ($q = 0$), exponential Shannon entropy ($q = 1$), and inverse Simpson index ($q = 2$) are united using the parameter q, which specifies the

sensitivity of the parameter to the relative abundance of genera, with richness ($q = 0$) insensitive to changes in frequency and Hill numbers of order $q = 2$ the most sensitive to the frequency of genera.

Comparing raw diversity data is inadvisable since estimates are sensitive to sampling intensity/sample size and completeness [117]. To account for differences in sampling intensity, we calculated asymptotic diversity estimates based on rarefaction-extrapolation curves, extrapolating to twice the number of observations of the reference sample (i.e., the time period with the greater observation N) with confidence intervals calculated via bootstrapping (n = 200) [117]. Within each ecoregion, we treated each observation as an occurrence of a particular genus, generating frequency estimates for each genus within a particular ecoregion (incidence data). Diversity patterns were analyzed at the ecoregion level, since these areas are similar in terms of environmental conditions and stressors, and comparing diversity patterns among them may help generate hypotheses regarding mechanisms driving changes. Moreover, generating diversity estimates based on ecological rather than purely spatial (i.e., pixels) boundaries improves accuracy. Samples were rarefied, or observations randomly removed, in order to calculate richness across the same overall sampling intensity (total number of observations at each ecoregion). To extend sampling curves beyond observed occurrences, diversity metrics were extrapolated using sample completeness, a method that estimates false absences based on the number of rare species within an assemblage [118].

Data limitations and biases

Our approach can be used to detect changes in records of the same taxa over time as well as to infer knowledge gaps and areas of under-sampling. The taxonomic lists we used for our final, coarse, all-potential-pollinator analysis (genera for invertebrates, species for vertebrates) are limited by the extent of our knowledge of organismal diets and behaviors. We do not have lists of all pollinators for all plants in North America, so there are certainly cryptic, rare, or undetected pollinators or pollinator groups that were not included in the lists of likely pollinators we used and thus in our GBIF extraction process. Likewise, our lists of genera likely included some cryptic or understudied groups that do not act as effective pollinators, since we included full genera that occurred on existing lists and overviews and were described as transporting pollen, even when the species within those genera have not been individually studied. Many invertebrate pollinators are exceedingly difficult to detect, catch, and identify, making even the extensive database of GBIF sparse for many taxonomic groups and biased toward more charismatic or visible taxa. Geographic locations are unevenly sampled across the study region. Locations that are remote, topographically complex, or far from human occupancy rarely receive the sampling intensity of locations that are easily accessible. An absence from a particular ecoregion or habitat, therefore, can be interpreted only as a lack of confirmed presence, rather than a true absence.

Results

Part 1: Patterns of spatial and temporal diversity: Apidae, Megachilidae, Pieridae, and Papilionidae

Ensemble species distribution models for the four focal charismatic families highlighted different hotspots of high species richness for those focal groups (Fig 1). Highest predicted species richness for the four groups combined occurred along the US West Coast, particularly in California and the Rocky Mountain region, with moderate richness in the Great Lakes and Atlantic seaboard. Time period comparisons among species distribution models for the four focal
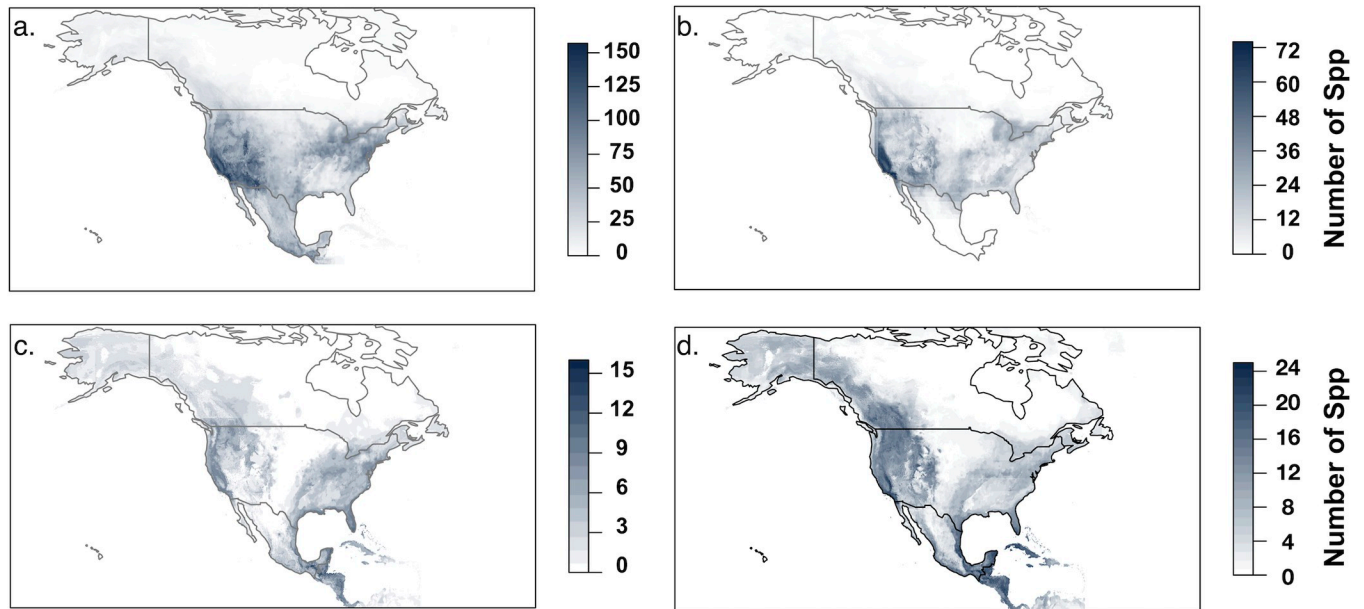
Fig 1. Overlay of species distribution models. Maps include projected distributions of all species from the four families (a) Apidae, (b) Megachilidae, (c) Papilionidae, and (d) Pieridae, depicting locations of highest diversity of species within these families across North America. Maps were created in R version 3.6.2 (R Core Development Team 2016) using thresholded and stacked results of species distribution models for each species, filtered to North American locations, and overlaid.

https://doi.org/10.1371/journal.pone.0289742.g001

families indicated that species richness has declined in western North America for all families and, for butterflies, in southern Mexico, and has increased for all families in eastern North America (Fig 2). Centroids of the predicted distributions of analyzed species shifted extensively during the two comparison time periods, with an arithmetic mean percent change for Apidae of 500 (95% CI 490 to 510) km, for Megachilidae of 625 (95% CI 616 to 635) km, for Papilionidae of 487 (95% CI 478 to 497) km, and for Pieridae of 351 (95% CI 342 to 361) km (S1 Fig). Direction of centroid movement varied by species but was most often toward the southeast (S2 Fig). The projected area of species distributions has also expanded substantially between the two time periods, with arithmetic mean percent changes of 137% for Apidae, 202% for Megachilidae, 153% for Papilionidae, and 148% for Pieridae (S3 Fig). Taken together, these findings indicate that in recent decades species' ranges within these four families have generally shifted southeastward and expanded. The shift and expansion across all four families is likely due to climatic and land-use changes, but other factors, including changes to how the underlying occurrence points were sampled, may be playing a role.

Part 2: Patterns of vulnerability: Species of concern

Records of species of concern were particularly frequent in areas of high human occupancy (the Great Lakes and US East Coast) and across southern Canada (Fig 3); this pattern again tracks areas of high human activity and may also indicate targeted sampling for rare species. Where more sampling is performed, it is more likely that managers and researchers will detect declines over time and thus determine that a species is of concern, and it is also more likely that rare species will be detected. At the same time, areas of high human activity are likely to exhibit high habitat loss and other environmental change, with impact to pollinator populations.
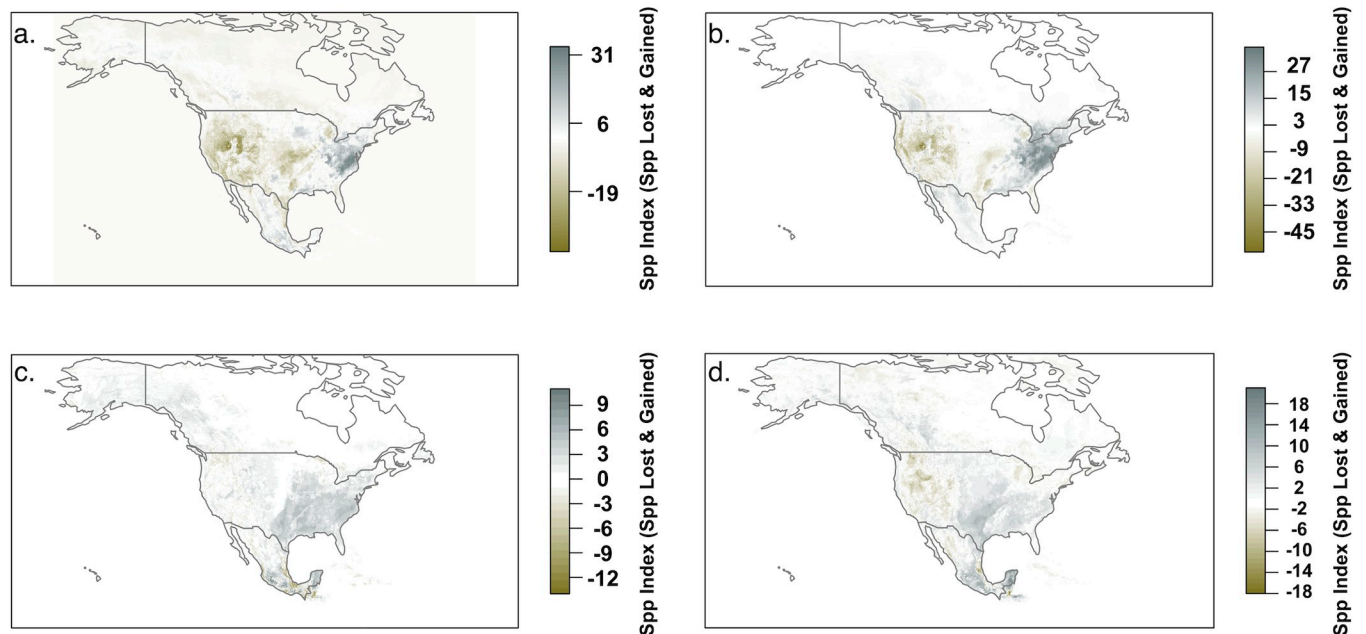
Fig 2. Maps of (a) Apidae, (b) Megachilidae, (c) Papilionidae, and (d) Pieridae species gains and losses within projected species distributions between 1980–2020 and 1939–1979. Thresholded species distribution model outputs from 1939–1979 were subtracted from those from 1980–2020 for all species, resulting in a map of a species distribution with three possible values: -1 (species projected in a given area in 1939–1979 but not 1980–2020), 0 (species projected in a given area in both time periods), and 1 (species projected in a given area in 1980–2020 but not 1939–1979). Each map is the result of the summation of these difference rasters for all species within each family. Areas displayed in gold represent locations where high numbers of species were projected to be lost from the first time period to the second. Dark gray areas represent locations where high numbers of species were projected to be gained from the first time period to the second. Maps were created in R version 3.6.2 (R Core Development Team 2016) using thresholded and stacked results of species distribution models for each species, filtered to North American locations, and overlaid.

https://doi.org/10.1371/journal.pone.0289742.g002

Part 3: Diversity assessment of potential pollinator occurrence across North America

Analysis aimed at summarizing the distribution of records for all potential pollen carrying taxa included 262,921 observations of 2384 insect genera across the three countries. Across diversity indices, generic richness of potential pollinator occurrence records was highest in the EPA Level I Ecoregions Mediterranean California, Southern semiarid highlands, and Marine west coast forests (Figs 4, 5; S4 Table). When evenness is included in diversity estimates (H = 1, 2), the EPA Level I Ecoregions Hudson Plains and Arctic Cordillera also emerge as contemporary diversity hotspots (S4 Table).

When we examined shifts in generic diversity across all pollinator groups through time, all asymptotic estimates of diversity (H = 0, 1, 2) indicated decreases in diversity over time in Mediterranean California, Tropical Dry and Wet Forests, the Temperate Sierras, and the Southern Semiarid Highlands (EPA Level I Ecoregions; S4 Table). The number of observations differed by several orders of magnitude between time period 1 and 2 for several ecoregions, including the Arctic Cordillera, the Hudson Plains, and the Taiga, which experienced a 27-, 40-, and 3-fold increase in observations, respectively (S4 Table).

Discussion

The agreement between analyses performed at multiple taxonomic levels across all three parts of our study provides evidence that records of pollinators in at least four key groups (Apidae, Megachilidae, Pieridae, and Papilionidae) have experienced disproportionate increases in the
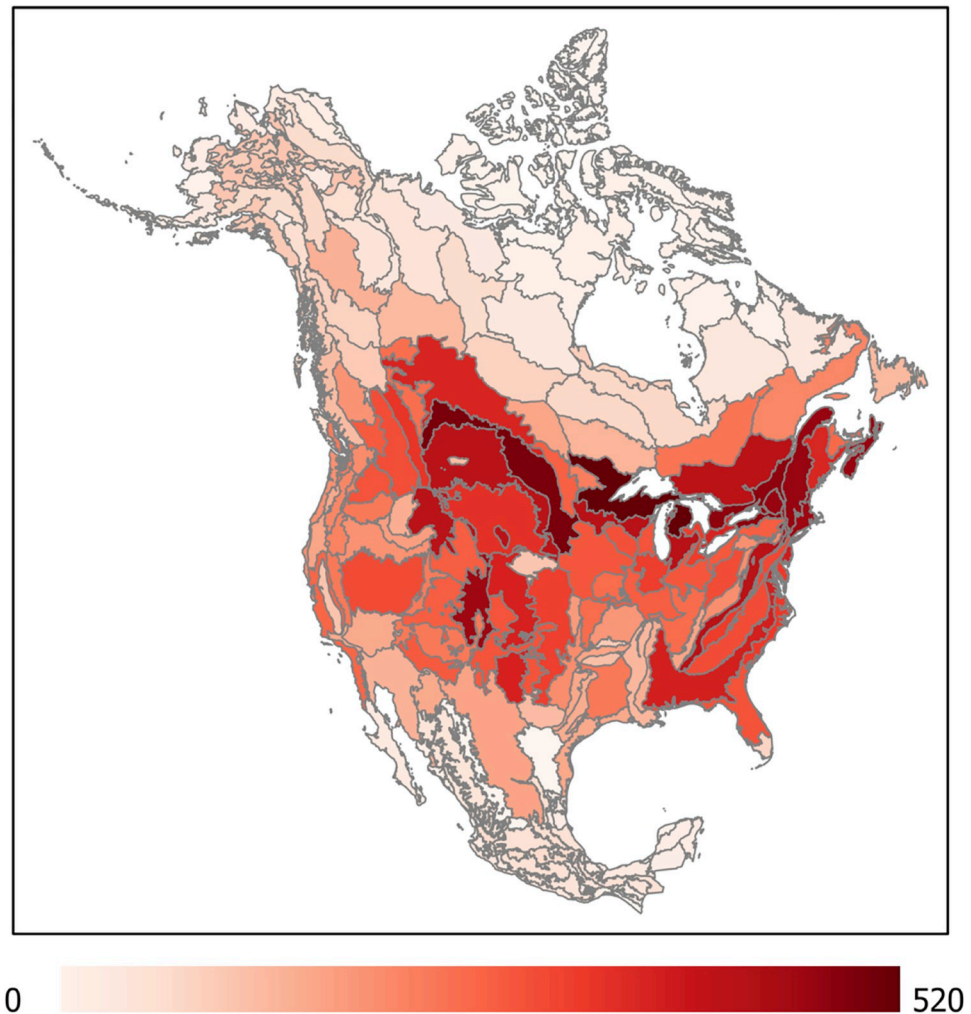
Fig 3. **Spatial distribution of occurrence records for likely pollinators that are listed as species of concern, represented by EPA Level III Ecoregions in North America.** (Map created in ArcGIS; basemap source: US Environmental Protection Agency, http://edg.epa.gov. Ecoregion reference map available at: https://gaftp.epa.gov/EPADataCommons/ORD/Ecoregions/us/Eco_Level_III_US.pdf).

https://doi.org/10.1371/journal.pone.0289742.g003

eastern and southeastern US relative to the western US and southern Mexico (Fig 5; S4 Table). Estimates of generic diversity also suggest declining diversity in the western US and tropical regions, while cooler, wetter areas, including the Arctic cordillera, Eastern temperate forests, Hudson plains, Marine west coast forests, Northern forests, Northwestern forested mountains, Taiga, and Tundra, have experienced an increase in pollinator diversity. The one exception to this pattern is the North American deserts ecoregion, where pollinator diversity increased.

Centroid shifting between time periods in SDMs could be due to the influence of sampling on the underlying datasets, the effect of climate change on species' occurrences, or both. An increase in citizen science and similar data collection efforts could have resulted in oversampling in the East in the second time period, which could then have resulted in the density of underlying presences "pulling" the centroid of the distribution in that direction for many species. Separating digital observations from other observations (i.e., traditional collections) reveals that detections using traditional methods began to decline for all four families in the 1960s although detections using digital observations, as expected, increased sharply after the
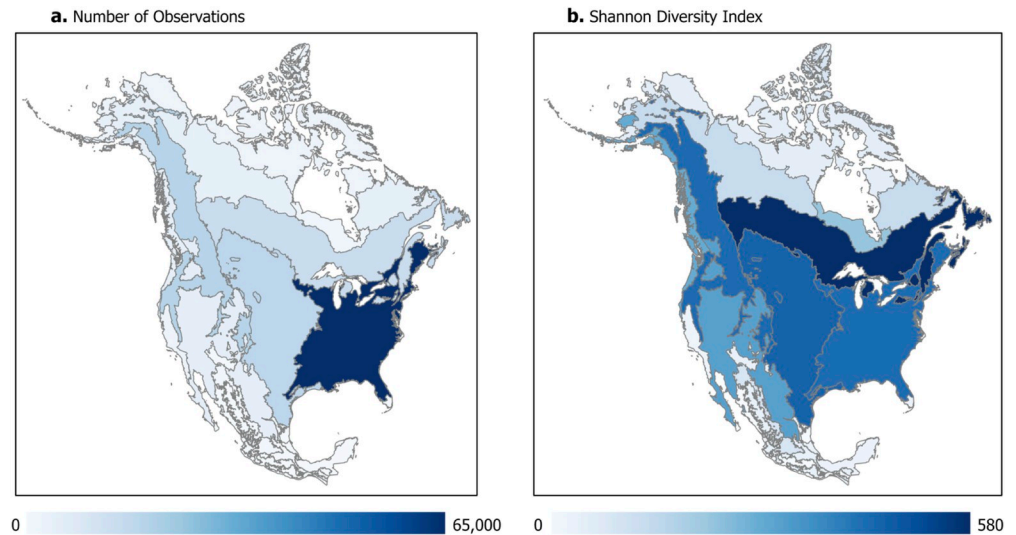
Fig 4. Potential pollinator records across North America. Records are summarized by (a) number of observations in existing GBIF records, and (b) Shannon diversity index within EPA Level 1 Ecoregions in North America. (Map created in ArcGIS; basemap source: US Environmental Protection Agency, http://edg.epa.gov. Ecoregion reference map available at: https://gaftp.epa.gov/EPADataCommons/ORD/Ecoregions/cec_na/NA_LEVEL_I.pdf).

https://doi.org/10.1371/journal.pone.0289742.g004

year 2000 (S4 Fig). Alternatively, a decades-long drought and associated habitat degradation in the West [119–121] could have pushed species' distributions east. Generally, both methods of assessing shifts in diversity presented here (i.e., SDM analyses and asymptotic diversity analyses) suggest climatic shifts are, at least in part, driving changes in pollinator diversity through time, as pollinators appear to track cooler, wetter conditions. Other factors, such as land use change, may also explain decreases in pollinator abundance observed in areas experiencing high rates of habitat conversion, like the Mediterranean California ecoregion.

Though asymptotic estimates of diversity and SDM approaches account for differences in sampling effort, three ecoregions exhibited order-of-magnitude increases in pollinator observations from time 1 to time 2. Estimates of diversity for these ecoregions, the Arctic Cordillera, the Hudson Plains, and the Taiga, may be inflated due to the sheer magnitude of increase in search effort (S4 Table). Such increased sampling could affect results in areas of high human population and activity (i.e., the eastern temperate forests) but given the high human density across California and parts of Mexico, it is unlikely that disparate sampling effort is the sole cause of unbalanced occurrence records. Instead, areas of reduced detection and high human occupancy may reveal the effects of environmental change on pollinator populations and diversity, particularly where habitat loss has been rapid and climate change-driven drought significant [122, 123]. The enormous number of records available in GBIF allows us to examine changes over time for key groups and to identify areas of particular vulnerability where species of concern are concentrated or richness of well-sampled pollinators has declined [124]. However, knowledge gaps are extensive. An absence from a particular ecoregion or habitat can be interpreted only as a lack of confirmed presence, rather than a true absence. Our use of SDMs reduces this bias but does not eliminate it, since SDMs are based in real occurrence data and thus limited by it in accuracy.

Current occurrence records for both species of concern and for the broad, all-inclusive set of potential pollinators in our final analysis are particularly diverse and abundant in the Great Plains, eastern temperate forests, Great Lakes region, and northern forests. The agreement between these datasets provides evidence that patterns are robust to taxonomic resolution and
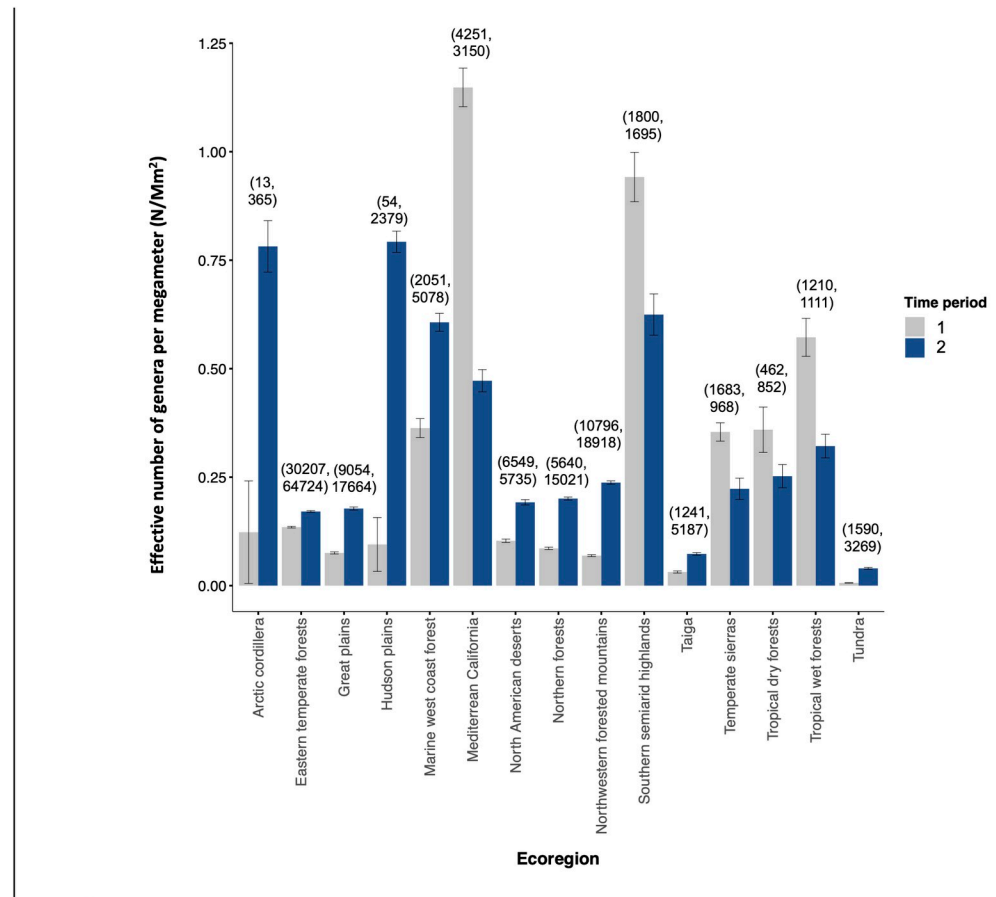
Fig 5. Asymptotic diversity estimates of order q = 1 (equivalent to exponential Shannon entropy) derived from rarefaction-extrapolation curves for each ecoregion (Level 1) relativized by land area (Mm^2) across two time periods (1939–1979; 1980–2020). Error bars indicate 95% confidence intervals calculated through bootstrapping (n = 200). Observation numbers are presented for each ecoregion above bars, with observations for time period 1 presented first, followed by observation numbers for time period 2. Although with the advent of smartphones and expansion of citizen science efforts detections have increased in most ecoregions, some ecoregions display declining detection between the two time periods.

https://doi.org/10.1371/journal.pone.0289742.g005

monitoring effort. Furthermore, this agreement suggests that the patterns of richness and declines found for genera in this study hold implications for species-level conservation and policy. As the number of people interested in and trained in natural history increases, sampling effort also increases, with biases toward locations that are most accessible. We therefore expected that records of most pollinator taxa would have increased over time, with steepest increases in well-sampled regions. Today, an increasing percentage of natural history observations are performed via smartphone, using apps such as iNaturalist and others [125]. Partitioning frequencies in detection using smartphones from detection using museum and herbarium specimens, which have remained constant or declined in recent years, can highlight taxa or geographies in which declines in abundance are in agreement across detection modes and therefore may represent true declines. We developed our species distribution models for four particularly well-known groups in order to address these potential sources of bias—taking advantage of the fact that these groups represent diverse life histories and habitat needs, and patterns within these groups may thus be reflective of less well-studied taxa with overlapping

requirements. We also employed methods to reduce error (e.g., spatial thinning) in these SDMs and overlaid the resulting spatial models to assess diversity across the study region.

In spite of data gaps and biases, our results hold implications for policy and management. Species distribution models imply increased presence in the East with potential range expansion for many pollinators in the US, with losses in the West. The western US contains large expanses of forests and rangelands that have been substantially altered over decades of fire suppression, overgrazing, recreation, and resource extraction [126–130]. Anthropogenic disturbances interacting with current and ongoing major drought result in widespread ecosystem degradation, loss of functional groups, and diminished biodiversity [131–135]. In southern Mexico, where SDMs also indicate decreased species richness, expansion of pasture and tree plantations have resulted in losses of native forest since the turn of the century [136]. These known environmental changes may help explain the pollinator range shifts and losses we detected here.

In response to these changes, policymakers and managers can prioritize pollinator habitat restoration. An active current area of research is techniques for and efficacy of such restoration efforts, which range from concentrated gardens of pollinator-friendly plants to broad, landscape-scale seeding with native flowering species [137–144]. Objectives of such restorations are to ensure consistent diversity and abundance of pollinator forage plants over the full growing season as well as availability of cover, protection, and pollinator nesting materials. Although managers are increasingly prioritizing such resources in restoration following disturbance, availability of native seed is limited and can lead to high restoration costs and delays, making pollinator-friendly seed production an additional priority area of need [145–147].

In addition to reductions in pollinators in regions facing broadscale environmental degradation, the current state of knowledge suggests that pollinators remain abundant and diverse in many developed and urban areas. This is encouraging and may reflect the fact that managed urban areas often contain added resources such as landscaping and garden plants, surface water features, and reduced predation [148–150]. Pollinator habitat within urban areas can be promoted by use of flowering plants in public spaces, public education to reduce pesticide application, and replacement of lawns with native plants spanning a diversity of functional groups. However, not all pollinators are equally successful in urban areas [149, 150], highlighting the need for pollinator conservation beyond areas of high human population density.

Our results join an expanding literature aiming to understand current and changing spatial patterns of diversity for potential pollinators, with an eye to identifying knowledge gaps and guiding future research to fill those gaps. Most notably, Chesshire and colleagues [23] recently projected and mapped bee species richness for the contiguous United States, finding that existing records are far from complete and that areas of high human density, particularly coastal regions and national parks, exhibit the highest levels of data completeness. A similar data completeness analysis was performed by Shirey and colleagues [151] for North American butterflies. Results suggested once again that butterflies are best-known in areas of high human population and high citizen science activity, and that under-sampling is particularly pronounced for certain taxonomic groups and for geographic areas with high climate change trajectories [151]. In addition to our primary focus—the time-period comparison we employed to assess shifting patterns of diversity for Apidae, Megachilidae, Pieridae, and Papilionidae—our work here complements these previous efforts in its identification of knowledge gaps by providing a broader lens that encompasses potential pollen-carriers such as flies, beetles, and non-bee Hymenoptera. These studies find broad agreement that systematic sampling across ecoregions and approaches to detect an increasing diversity of taxonomic groups are important to inform changes in invertebrate communities into the future.

Moving forward, improved pollinator sampling to detect declines should include enhanced methods of citizen science engagement, increased sampling of cryptic and elusive taxa, and improved ability to link pollinator diversity and occurrence to climate and vegetation metrics, in order to account for cryptic and more difficult-to-detect pollinator groups. Establishment of regular and systematic pollinator sampling in all Level I ecoregions, for example via monitoring stations or periodic bioblitzes, would help to standardize data collection across geographies and fill in important geographic knowledge gaps. Addressing knowledge gaps is challenging, but continued advancement in quantitative approaches as well as expanded and diversified data collection are key. Pollinators are perhaps the most intersectional biotic group of these times of global change: all human and non-human terrestrial communities rely upon them. Improving our ability to track and understand their declines will be critical to our assessment of food security and ecosystem services in the future.

Supporting information

S1 Table. Families of possible invertebrate pollinators for which GBIF records were extracted, along with example sources used to determine whether genera within each family have been recorded feeding on pollen, nectar, or flowers, and transporting pollen. Target families were identified using these and other sources (see main text) and then online sources including Discover Life, BugGuide, and Biosystematic Database of World Diptera were used to examine genera within the families for dietary and pollen-carrying details. (DOCX)

S2 Table. Vertebrate pollinators ranked as species of concern according to the IUCN Red List.
(DOCX)

S3 Table. Number of occurrences within each family for the time periods 1940–1979 (T1) and 1980–2020 (T2) that were used in building species distribution models.
(DOCX)

S4 Table. Asymptotic diversity indices (H = 0; Richness, H = 1; Shannon's, H = 2; Simpsons) for time periods 1 and 2 across Level 1 ecoregions. Total area (kilometers squared) of each ecoregion and number of observations for each time period are provided. Both diversity indices and observation numbers were also relativized by Ecoregion area and expressed as N *per* Mega meter (1000 Km) squared. For each diversity index, 95% confidence intervals are provided below the value in parentheses.
(DOCX)

S1 Fig. The distance that the centroid of projected species' ranges moved between 1940–1979 and 1980–2020. Bee species are represented by circles (Apidae) and triangles (Megachilidae), and butterfly species are represented by diamonds (Papilionidae) and squares (Pieridae). Distance for all species is shown with the y-axis on a log scale to account for the wide range of values. Arithmetic mean percent change in projected area of the species' distributions for each family are represented by colored lines, yellow for bees (Apidae (500 km) and Megachilidae (625 km)) and blue for butterflies (Papilionidae (487 km) and Pieridae (351 km)). Changes are likely a consequence of both disproportionately increased detection in some areas of the range and decreased occurrence in other areas. Figure was created in R version 3.6.2 (R package 'geosphere' by Hijmans et al. 2021; R Core Team 2020).
(DOCX)

S2 Fig. Latitudinal and longitudinal change of the centroid from 1940–1979 to 1980–2020 of the project species' ranges for the two bee families (displayed in yellow) and two butterfly families (blue). To calculate the change of the centroid of projected species' ranges, we subtracted the coordinates of the centroid for 1940–1979 from the coordinates of the centroid for 1980–2020. To represent the change in location of the centroid, the blunt ends of the arrows are positioned at (0,0) and the pointed end of each arrow is positioned at the calculated difference in longitude and latitude. Each arrow represents one species within the family. Figure was created in R version 3.6.2 (R package 'geosphere' by Hijmans et al. 2021; R Core Team 2020).
(DOCX)

S3 Fig. Percent change in the projected area of the species' distributions of all pollinator species between the time periods 1939–1979 and 1980–2020. Bee species are represented by circles (Apidae) and triangles (Megachilidae), and butterfly species are represented by diamonds (Papilionidae) and squares (Pieridae). Percent change for all species is shown with the y-axis on a log scale to account for the wide range of values. Arithmetic mean percent change in projected area of the species' distributions for each family are represented by colored lines, yellow for bees (Apidae (137%) and Megachilidae (202%)) and blue for butterflies (Papilionidae (153%) and Pieridae (148%)). A dashed line is shown at 100%, representing no change between the two time periods. Any species with points below this dashed line experienced a decrease in their projected distributions from 1939–1979 to 1920–2020, and any species with points above this dashed line experienced an increase in their projected distributions. The mean percent change for all families was >100%. Figure was created in R version 3.6.2 (R package 'geosphere' by Hijmans et al. 2021; R Core Team 2020).
(DOCX)

S4 Fig. Observations of genera through time (each line indicates 1 genus). Detections using traditional methods (grey) were variable through time, with declines after 2014, although digital methods of observation generally increased in the 2000s.
(DOCX)

Acknowledgments

Author Contributions

Conceptualization: Clare E. Aslan.

Data curation: Sara K. Souther, Manette E. Sandor.

Formal analysis: Sara K. Souther, Manette E. Sandor.

Funding acquisition: Clare E. Aslan.

Investigation: Martha Sample, Sara Gabrielson.

Methodology: Sara K. Souther, Clare E. Aslan.

Project administration: Clare E. Aslan.

Visualization: Sara K. Souther.

Writing – original draft: Sara K. Souther, Manette E. Sandor, Martha Sample, Sara Gabriel-son, Clare E. Aslan.

References

1. Ollerton J, Winfree R, Tarrant S. How many flowering plants are pollinated by animals? Oikos. 2011; 120: 321–326. https://doi.org/10.1111/j.1600-0706.2010.18644.x

2. Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE. Global pollinator declines: trends, impacts and drivers. Trends Ecol Evol. 2010; 25: 345–353. https://doi.org/10.1016/j.tree.2010.01.007 PMID: 20188434

3. Pauw A, Hawkins JA. Reconstruction of historical pollination rates reveals linked declines of pollinators and plants. Oikos. 2011; 120: 344–349. https://doi.org/10.1111/j.1600-0706.2010.19039.x

4. Lebuhn G, Droege S, Connor EF, Gemmill-Herren B, Potts SG, Minckley RL, et al. Detecting insect pollinator declines on regional and global scales. Conserv Biol. 2013; 27: 113–120. https://doi.org/10.1111/j.1523-1739.2012.01962.x PMID: 23240651

5. Vanbergen AJ, Initiative the IP. Threats to an ecosystem service: pressures on pollinators. Front Ecol Environ. 2013; 11: 251–259. https://doi.org/10.1890/120126

6. Goulson D, Nicholls E, Botías C, Rotheray EL. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science. 2015; 347: 1255957. https://doi.org/10.1126/science.1255957 PMID: 25721506

7. Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, et al. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science. 2006; 313: 351–354. https://doi.org/10.1126/science.1127863 PMID: 16857940

8. Cameron SA, Lozier JD, Strange JP, Koch JB, Cordes N, Solter LF, et al. Patterns of widespread decline in North American bumble bees. Proc Natl Acad Sci. 2011; 108: 662–667. https://doi.org/10.1073/pnas.1014743108 PMID: 21199943

9. Aslan CE, Zavaleta ES, Tershy B, Croll D, Robichaux RH. Imperfect replacement of native species by non-native species as pollinators of endemic Hawaiian plants. Conserv Biol. 2014; 28: 478–488. https://doi.org/10.1111/cobi.12193 PMID: 24372761

10. Garibaldi LA, Carvalheiro LG, Leonhardt SD, Aizen MA, Blaauw BR, Isaacs R, et al. From research to action: enhancing crop yield through wild pollinators. Front Ecol Environ. 2014; 12: 439–447. https://doi.org/10.1890/130330

11. Archer CR, Pirk CWW, Carvalheiro LG, Nicolson SW. Economic and ecological implications of geographic bias in pollinator ecology in the light of pollinator declines. Oikos. 2014; 123: 401–407. https://doi.org/10.1111/j.1600-0706.2013.00949.x

12. Bartomeus I, Stavert JR, Ward D, Aguado O. Historical collections as a tool for assessing the global pollination crisis. Philos Trans R Soc B Biol Sci. 2019; 374: 20170389. https://doi.org/10.1098/rstb.2017.0389 PMID: 30455207

13. Hall DM, Martins DJ. Human dimensions of insect pollinator conservation. Curr Opin Insect Sci. 2020; 38: 107–114. https://doi.org/10.1016/j.cois.2020.04.001 PMID: 32375115

14. Hall DM, Steiner R. Insect pollinator conservation policy innovations at subnational levels: Lessons for lawmakers. Environ Sci Policy. 2019; 93: 118–128. https://doi.org/10.1016/j.envsci.2018.12.026

15. Drivdal L, van der Sluijs JP. Pollinator conservation requires a stronger and broader application of the precautionary principle. Curr Opin Insect Sci. 2021; 46: 95–105. https://doi.org/10.1016/j.cois.2021.04.005 PMID: 33930597

16. Nicotra AB, Beever EA, Robertson AL, Hofmann GE, O'Leary J. Assessing the components of adaptive capacity to improve conservation and management efforts under global change. Conserv Biol. 2015; 29: 1268–1278. https://doi.org/10.1111/cobi.12522 PMID: 25926277

17. Beever EA, O'Leary J, Mengelt C, West JM, Julius S, Green N, et al. Improving conservation outcomes with a new paradigm for understanding species' fundamental and realized adaptive capacity. Conserv Lett. 2016; 9: 131–137. https://doi.org/10.1111/conl.12190

18. Aitken SN, Whitlock MC. Assisted gene flow to facilitate local adaptation to climate change. Annu Rev Ecol Evol Syst. 2013; 44: 367–388. https://doi.org/10.1146/annurev-ecolsys-110512-135747

19. Wilcock C, Neiland R. Pollination failure in plants: why it happens and when it matters. Trends Plant Sci. 2002; 7: 270–277. https://doi.org/10.1016/s1360-1385(02)02258-6 PMID: 12049924

20. Fantinato E, Del Vecchio S, Gaetan C, Buffa G. The resilience of pollination interactions: importance of temporal phases. J Plant Ecol. 2019; 12: 157–162. https://doi.org/10.1093/jpe/rty005

21. Oliver TH, Heard MS, Isaac NJB, Roy DB, Procter D, Eigenbrod F, et al. Biodiversity and resilience of ecosystem functions. Trends Ecol Evol. 2015; 30: 673–684. https://doi.org/10.1016/j.tree.2015.08.009 PMID: 26437633

22. Millennium Ecosystem Assessment (Program), editor. Ecosystems and human well-being: synthesis. Washington, DC: Island Press; 2005.

23. Chesshire PR, Fischer EE, Dowdy NJ, Griswold TL, Hughes AC, Orr MC, et al. Completeness analysis for over 3000 United States bee species identifies persistent data gap. Ecography. n/a: e06584. https://doi.org/10.1111/ecog.06584

24. Bird TJ, Bates AE, Lefcheck JS, Hill NA, Thomson RJ, Edgar GJ, et al. Statistical solutions for error and bias in global citizen science datasets. Biol Conserv. 2014; 173: 144–154. https://doi.org/10.1016/j.biocon.2013.07.037

25. Beck J, Böller M, Erhardt A, Schwanghart W. Spatial bias in the GBIF database and its effect on modeling species' geographic distributions. Ecol Inform. 2014; 19: 10–15. https://doi.org/10.1016/j.ecoinf.2013.11.002

26. Becken S, Connolly RM, Chen J, Stantic B. A hybrid is born: Integrating collective sensing, citizen science and professional monitoring of the environment. Ecol Inform. 2019; 52: 35–45. https://doi.org/10.1016/j.ecoinf.2019.05.001

27. GBIF: The Global Biodiversity Information Facility. What is GBIF? 2022. Available: https://www.gbif.org/what-is-gbif [13 January 2020].

28. Michener CD. The bees of the world. JHU Press; 2000.

29. Luis-Martínez A, García AS, Ávalos-Hernández O, Salinas-Gutiérrez JL, Trujano-Ortega M, Arellano-Covarrubias A, et al. Distribution and diversity of Papilionidae and Pieridae (Lepidoptera: Papilionoidea) in Loxicha Region, Oaxaca, Mexico. Rev Biol Trop. 68: 139–155.

30. Monteagudo Sabaté D, Luis Martínez MA. Altitudinal richness patterns of Papilionidae, Pieridae and Nymphalidae (Lepidoptera) in Mexican mountain areas. Rev Biol Trop. 2013; 61. Available: https://pubmed.ncbi.nlm.nih.gov/24027939/

31. Carter D. Butterflies and moths. Dorling Kindersley; 2000.

32. Yesson C, Brewer PW, Sutton T, Caithness N, Pahwa JS, Burgess M, et al. How global is the global biodiversity information facility? PloS One. 2007; 2: e1124. https://doi.org/10.1371/journal.pone.0001124 PMID: 17987112

33. Omernik JM. Ecoregions: A framework for managing ecosystems. George Wright Forum. 1995; 12: 35–50.

34. Omernik JM. Ecoregions of the conterminous United States. Ann Assoc Am Geogr. 1987; 77: 118–125.

35. Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. Very high resolution interpolated climate surfaces for global land areas. Int J Climatol. 2005; 25: 1965–1978. https://doi.org/10.1002/joc.1276

36. VanDerWal J, Shoo LP, Graham C, Williams SE. Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? Ecol Model. 2009; 220: 589–594. https://doi.org/10.1016/j.ecolmodel.2008.11.010

37. Barbet-Massin M, Jiguet F, Albert CH, Thuiller W. Selecting pseudo-absences for species distribution models: how, where and how many? Methods Ecol Evol. 2012; 3: 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x

38. Naimi B, Hamm NAS, Groen TA, Skidmore AK, Toxopeus AG. Where is positional uncertainty a problem for species distribution modelling? Ecography. 2014; 37: 191–203. https://doi.org/10.1111/j.1600-0587.2013.00205.x

39. Naimi B, Araújo MB. sdm: a reproducible and extensible R platform for species distribution modelling. Ecography. 2016; 39: 368–375. https://doi.org/10.1111/ecog.01881

40. Araújo MB, New M. Ensemble forecasting of species distributions. Trends Ecol Evol. 2007; 22: 42–47. https://doi.org/10.1016/j.tree.2006.09.010 PMID: 17011070

41. Buisson L, Thuiller W, Casajus N, Lek S, Grenouillet G. Uncertainty in ensemble forecasting of species distribution. Glob Change Biol. 2010; 16: 1145–1157. https://doi.org/10.1111/j.1365-2486.2009.02000.x

42. Thuiller W, Guéguen M, Renaud J, Karger DN, Zimmermann NE. Uncertainty in ensembles of global biodiversity scenarios. Nat Commun. 2019; 10: 1446. https://doi.org/10.1038/s41467-019-09519-w PMID: 30926936

43. Hao T, Elith J, Lahoz-Monfort JJ, Guillera-Arroita G. Testing whether ensemble modelling is advantageous for maximising predictive performance of species distribution models. Ecography. 2020; 43: 549–558. https://doi.org/10.1111/ecog.04890

44. Konowalik K, Nosol A. Evaluation metrics and validation of presence-only species distribution models based on distributional maps with varying coverage. Sci Rep. 2021; 11: 1482. https://doi.org/10.1038/s41598-020-80062-1 PMID: 33452285

45. Liu C, Berry PM, Dawson TP, Pearson RG. Selecting thresholds of occurrence in the prediction of species distributions. Ecography. 2005; 28: 385–393. https://doi.org/10.1111/j.0906-7590.2005.03957.x

46. Jay A, Reidmiller D, Avery C, Barrie D, DeAngelo B, Dave A, et al. The Fourth National Climate Assessment: Summary findings and overview. Earth Space Sci Open Arch ESSOAr. 2019.

47. Rapaport RA, Urban NR, Capel PD, Baker JE, Looney BB, Eisenreich SJ, et al. "New" DDT inputs to North America: Atmospheric deposition. Chemosphere. 1985; 14: 1167–1173. https://doi.org/10.1016/0045-6535(85)90138-9

48. Pham T, Lum K, Lemieux C. The occurrence, distribution and sources of DDT in the St. Lawrence River, Quebec (Canada). Chemosphere. 1993; 26: 1595–1606. https://doi.org/10.1016/0045-6535(93)90105-E

49. Pérez-Maldonado IN, Trejo A, Ruepert C, Jovel R del C, Méndez MP, Ferrari M, et al. Assessment of DDT levels in selected environmental media and biological samples from Mexico and Central America. Chemosphere. 2010; 78: 1244–1249. https://doi.org/10.1016/j.chemosphere.2009.12.040 PMID: 20092871

50. Hijmans RJ, Phillips S, Leathwick J, Elith J. dismo: Species distribution modeling. R package version 1.3–5. 2021.

51. Messina JP, Brady OJ, Golding N, Kraemer MUG, Wint GRW, Ray SE, et al. The current and future global distribution and population at risk of dengue. Nat Microbiol. 2019; 4: 1508–1515. https://doi.org/10.1038/s41564-019-0476-8 PMID: 31182801

52. Riley J, Zeale M r. k., Razgour O, Turpin J, Jones G. Predicting the past, present and future distributions of an endangered marsupial in a semi-arid environment. Anim Conserv. 2021; 24: 890–903. https://doi.org/10.1111/acv.12696

53. Hijmans RJ. geosphere: Spherical Trigonometry. R package version 1.5–14. 2021.

54. Merckx T, Huertas B, Basset Y, Thomas J. A global perspective on conserving butterflies and moths and their habitats. Key topics in conservation biology 2. John Wiley & Sons, Ltd. 2013; 237–257.

55. Bush MB, Rivera R. Reproductive ecology and pollen representation among neotropical trees. Glob Ecol Biogeogr. 2001; 10: 359–367. https://doi.org/10.1046/j.1466-822X.2001.00247.x

56. Parker AJ. The ecological context of pollination: variation in an apparent mutualism. University of Toronto (Canada); 2014.

57. Castellanos MC, Wilson P, Thomson JD. 'Anti-bee' and 'pro-bird' changes during the evolution of hummingbird pollination in Penstemon flowers. J Evol Biol. 2004; 17: 876–885. https://doi.org/10.1111/j.1420-9101.2004.00729.x PMID: 15271088

58. Ollerton J, Alarcón R, Waser NM, Price MV, Watts S, Cranmer L, et al. A global test of the pollination syndrome hypothesis. Ann Bot. 2009; 103: 1471–1480. https://doi.org/10.1093/aob/mcp031 PMID: 19218577

59. Ne'eman G, Jürgens A, Newstrom-Lloyd L, Potts SG, Dafni A. A framework for comparing pollinator performance: effectiveness and efficiency. Biol Rev. 2010; 85: 435–451. https://doi.org/10.1111/j.1469-185X.2009.00108.x PMID: 20015317

60. Aslan CE, Shiels AB, Haines W, Liang CT. Non-native insects dominate daytime pollination in a high-elevation Hawaiian dryland ecosystem. Am J Bot. 2019; 106: 313–324. https://doi.org/10.1002/ajb2.1233 PMID: 30768870

61. Alarcón R, Waser NM, Ollerton J. Year-to-year variation in the topology of a plant–pollinator interaction network. Oikos. 2008; 117: 1796–1807. https://doi.org/10.1111/j.0030-1299.2008.16987.x

62. Aslan CE, Zavaleta ES, Tershy B, Croll D. Mutualism disruption threatens global plant biodiversity: a systematic review. PLoS ONE. 2013; 8. https://doi.org/10.1371/journal.pone.0066993 PMID: 23840571

63. Arnett RH Jr. American insects: a handbook of the insects of America north of Mexico. Crc Press; 2000.

64. Bailey P. Pollination biology of the endemic *Erigeron lemmonii* A. Gray, and its insect visitor networks compared to two widespread congeners *Erigeron arisolius* GL Nesom and *Erigeron neomexicanus* A. Gray (Asteraceae). PhD Thesis. 2013.

65. Beattie AJ, Breedlove DE, Ehrlich PR. The ecology of the pollinators and predators of *Frasera speciosa*. Ecology. 1973; 54: 81–91. https://doi.org/10.2307/1934376

66. Bernhardt P. Convergent evolution and adaptive radiation of beetle-pollinated angiosperms. Converg Evol. 1999; 28.

67. Blair AW, Williamson PS. Effectiveness and importance of pollinators to the star cactus (*Astrophytum asterias*). Southwest Nat. 2008; 53: 423–431.

68. Boldt PE, Robbins TO. Phytophagous and pollinating insect fauna of *Baccharis neglecta* (Compositae) in Texas. Environ Entomol. 1987; 16: 887–895. https://doi.org/10.1093/ee/16.4.887

69. Buchele DE, Baskin JM, Baskin CC. Ecology of the endangered species *Solidago shortii*. IV. Pollination ecology. Bull Torrey Bot Club. 1992; 137–141.

70. Carbone LM, Tavella J, Pausas JG, Aguilar R. A global synthesis of fire effects on pollinators. Glob Ecol Biogeogr. 2019; 28: 1487–1498. https://doi.org/10.1111/geb.12939

71. Dilley JD, Wilson P, Mesler MR. The radiation of *Calochortus*: generalist flowers moving through a mosaic of potential pollinators. Oikos. 2000; 89: 209–222. https://doi.org/10.1034/j.1600-0706.2000.890201.x

72. Evenhuis NL, Greathead DJ. World catalog of bee flies (Diptera: Bombyliidae): Corrigenda and addenda. Zootaxa. 2003; 300: 1. https://doi.org/10.11646/zootaxa.300.1.1

73. Figueroa-Castro DM, González-Tochihuitl G, Ramírez-Morales M del C, Rivas-Arancibia SP, Castaño-Meneses G. Insect visitors to the annual plant community in a xeric environment in Central Mexico. Fla Entomol. 2017; 100: 708–717. https://doi.org/10.1653/024.100.0417

74. Grant V, Grant KA, Hurd PD. Pollination of *Opuntia lindheimeri* and related species. Plant Syst Evol. 1979; 132: 313–320.

75. Hahn M, Brühl CA. The secret pollinators: an overview of moth pollination with a focus on Europe and North America. Arthropod-Plant Interact. 2016; 10: 21–28. https://doi.org/10.1007/s11829-016-9414-3

76. Hoebeke ER, Wheeler AG Jr. *Dasytes plumbeus* (Müller) (Coleoptera: Melyridae: Dasytinae), a Palearctic soft-winged flower beetle new to North America. Zootaxa. 2013; 3717: 377. https://doi.org/10.11646/zootaxa.3717.3.7 PMID: 26176113

77. Jakubska A, Kadej M, Prz D, Steininger A. Pollination ecology of *Epipactis helleborine* (L.) Crantz (Orchidaceae, Neottieae) in the south-western Poland. 2005; 15.

78. Kearns CA. North American dipteran pollinators: assessing their value and conservation status. Conserv Ecol. 2001; 5: art5. https://doi.org/10.5751/ES-00262-050105

79. Kevan PG. Insect pollination of high Arctic flowers. J Ecol. 1972; 60: 831–847. https://doi.org/10.2307/2258569

80. Koschnitzke C. Polinizadores e visitantes florais de três táxons de Asclepiadoideae (Apocynaceae) na restinga de Maricá, Rio de Janeiro, Brasil. 2015; 12.

81. Larson BMH, Kevan PG, Inouye DW. Flies and flowers: taxonomic diversity of anthophiles and pollinators. Can Entomol. 2001; 133: 439–465. https://doi.org/10.4039/Ent133439-4

82. Lemaitre AB, Pinto CF, Niemeyer HM. Generalized pollination system: Are floral traits adapted to different pollinators? Arthropod-Plant Interact. 2014; 8: 261–272.

83. Martínez-Adriano CA, Romero-Méndez U, Flores J, Jurado E, Estrada-Castillón E. Floral visitors of *Astrophytum myriostigma* in La Sierra El Sarnoso, Durango, Mexico. Southwest Nat. 2015; 60: 158–166.

84. Mawdsley JR. The importance of species of Dasytinae (Coleoptera: Melyridae) as pollinators in Western North America. Coleopt Bull. 2003; 57: 154–160. https://doi.org/10.1649/541

85. Council NR. Status of pollinators in North America. National Academies Press; 2007.

86. O'Hara JE, Wood DM. Catalogue of the Tachinidae (Diptera) of America north of Mexico. Associated Publishers; 2003.

87. Orford KA, Vaughan IP, Memmott J. The forgotten flies: the importance of non-syrphid Diptera as pollinators. Proc R Soc B Biol Sci. 2015; 282: 20142934. https://doi.org/10.1098/rspb.2014.2934 PMID: 25808886

88. Oriani A, Sano PT, Scatena VL. Pollination biology of *Syngonanthus elegans* (Eriocaulaceae–Poales). Aust J Bot. 2009; 57: 94–105. https://doi.org/10.1071/BT08119

89. Peña JE, Sharp JL, Wysoki M. Tropical fruit pests and pollinators: biology, economic importance, natural enemies, and control. CABI; 2002.

90. Player G. Pollination and wind dispersal of pollen in *Arceuthobium*. Ecol Monogr. 1979; 49: 73–87. https://doi.org/10.2307/1942573

91. Pohl GR, andry J-F, Schmidt BC, deWaard JR. Lepidoptera of Canada. ZooKeys. 2019; 463–505. https://doi.org/10.3897/zookeys.819.27259 PMID: 30713459

92. Pohl GR, Patterson B, Pelham JP. Annotated taxonomic checklist of the Lepidoptera of North America, North of Mexico. Work Pap Publ Online Authors. 2016.

93. Rader R, Bartomeus I, Garibaldi LA, Garratt MPD, Howlett BG, Winfree R, et al. Non-bee insects are important contributors to global crop pollination. Proc Natl Acad Sci. 2016; 113: 146–151. https://doi.org/10.1073/pnas.1517092112 PMID: 26621730

94. Roitman GG. Pollination biology of *Grindelia covasii* (Asteraceae), a potential crop for arid lands. J Arid Environ. 1999; 43: 103–110.

95. Ssymank A, Kearns CA, Pape T, Thompson FC. Pollinating Flies (Diptera): A major contribution to plant diversity and agricultural production. Biodiversity. 2011 [cited 30 Nov 2019]. Available: https://www.tandfonline.com/doi/pdf/10.1080/14888386.2008.9712892?needAccess=true

96. Stout JC, Kells AR, Goulson D. Pollination of the invasive exotic shrub *Lupinus arboreus* (Fabaceae) by introduced bees in Tasmania. Biol Conserv. 2002; 106: 425–434. https://doi.org/10.1016/S0006-3207(02)00046-0

97. Travis J. Breeding system, pollination, and pollinator limitation in a perennial herb, *Amianthium muscaetoxicum* (Liliaceae). Am J Bot. 1984; 71: 941–947. https://doi.org/10.2307/2443664

98. Werle C. Insects Associated with Southern Magnolia (*Magnolia grandiflora* L.) in East Tennessee. Masters Theses. 2002. Available: https://trace.tennessee.edu/utk_gradthes/2096

99. Wiesenborn WD. conspecific pollen on honey bees and a chrysomelid beetle species visiting female flowers on *Nolina microcarpa* (Asparagaceae). West North Am Nat. 2018; 78: 133–142. https://doi.org/10.3398/064.078.0204

100. Cai C, Escalona HE, Li L, Yin Z, Huang D, Engel MS. Beetle pollination of cycads in the Mesozoic. Curr Biol. 2018; 28: 2806–2812.e1. https://doi.org/10.1016/j.cub.2018.06.036 PMID: 30122529

101. Xiong W, Ollerton J, Liede-Schumann S, Zhao W, Jiang Q, Sun H, et al. Specialized cockroach pollination in the rare and endangered plant *Vincetoxicum hainanense* in China. Am J Bot. 2020; 107: 1355–1365.

102. Procheş Ş, Johnson SD. Beetle pollination of the fruit-scented cones of the South African cycad *Stangeria eriopus*. Am J Bot. 2009; 96: 1722–1730.

103. Vlasáková B, Pinc J, Jůna F, Kotyková Varadínová Z. Pollination efficiency of cockroaches and other floral visitors of *Clusia blattophila*. Plant Biol. 2019; 21: 753–761. https://doi.org/10.1111/plb.12956 PMID: 30620429

104. Heiduk A, Meve U, Menzel F, Haenni J-P, Tschirnhaus M von, Dötterl S, et al. Fly pollination of kettle trap flowers of *Riocreuxia torulosa* (Ceropegieae-Anisotominae): A generalized system of floral deception. Plants. 2021; 10: 1564. https://doi.org/10.3390/plants10081564 PMID: 34451609

105. Sharma MV, Armstrong JE. Pollination of *Myristica* and other nutmegs in natural populations. Trop Conserv Sci. 2013; 6: 595–607.

106. Pisciotta S, Raspi A, Sajeva M. First records of pollinators of two co-occurring Mediterranean Apocynaceae. Plant Biosyst—Int J Deal Asp Plant Biol. 2011; 145: 141–149. https://doi.org/10.1080/11263504.2010.540779

107. Hamley S. Plant-insect interactions in a riparian grassland: a community approach to pollination. PhD Thesis, Durham University. 1993.

108. Kevan PG, Baker HG. Insects as flower visitors and pollinators. Annu Rev Entomol. 1983; 28: 407–453. https://doi.org/10.1146/annurev.en.28.010183.002203

109. Wäckers FL, Romeis J, van Rijn P. Nectar and pollen feeding by insect herbivores and implications for multitrophic interactions. Annu Rev Entomol. 2007; 52: 301–323. https://doi.org/10.1146/annurev.ento.52.110405.091352 PMID: 16972766

110. Alameda D, Hidalgo BF, Rijo G, de Vales Fernández D, Castañeda A, Leyva LM. Diurnal pollination network of "Cuabales de Cajálbana", a serpentine shrubwood in western Cuba—Red diurna de polinización de "Cuabales de Cajálbana", un matorral xeromorfo sobre serpentina de Cuba occidental. Rev Jardín Botánico Nac. 2020; 41: 25–30.

111. Inouye DW, Ogilvie JE. Pollinators, Role of. Reference module in life sciences. Elsevier; 2017. pp. 140–146. https://doi.org/10.1016/B978-0-12-809633-8.02309–8

112. Wiesenborn WD, Heydon SL, Lorenzen K. Pollen loads on adult insects from tamarisk flowers and inferences about larval habitats at Topock Marsh, Arizona. J Kans Entomol Soc. 2008; 81: 50–60. https://doi.org/10.2317/JKES-705-15.1

113. Del Toro I, Ribbons RR, Pelini SL. The little things that run the world revisited: a review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). Myrmecol News. 2012; 17: 133–146.

114. Ramírez-Benavides W, Jansen-Gonzàles S. Flower visitation of *Passiflora apetala*, *P. auriculata* and *P. holosericea* (Passifloraceae) by *Pepsis aquila* (Hymenoptera: Pompilidae). Fragm Entomol. 2018; 50: 57–59. https://doi.org/10.13133/2284-4880/286

115. Hall MA, Reboud EL. High sampling effectiveness for non-bee flower visitors using vane traps in both open and wooded habitats. Austral Entomol. 2019; 58: 836–847. https://doi.org/10.1111/aen.12416

116. Hill MO. Diversity and evenness: a unifying notation and its consequences. Ecology. 1973; 54: 427–432. https://doi.org/10.2307/1934352

117. Chao A, Jost L. Coverage-based rarefaction and extrapolation: standardizing samples by complete-ness rather than size. Ecology. 2012; 93: 2533–2547. https://doi.org/10.1890/11-1952.1 PMID: 23431585

118. Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, et al. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol Monogr. 2014; 84: 45–67. https://doi.org/10.1890/13-0133.1

119. Duniway MC, Pfennigwerth AA, Fick SE, Nauman TW, Belnap J, Barger NN. Wind erosion and dust from US drylands: a review of causes, consequences, and solutions in a changing world. Ecosphere. 2019; 10: e02650. https://doi.org/10.1002/ecs2.2650

120. El-Vilaly MAS, Didan K, Marsh SE, van Leeuwen WJD, Crimmins MA, Munoz AB. Vegetation produc-tivity responses to drought on tribal lands in the four corners region of the Southwest USA. Front Earth Sci. 2018; 12: 37–51. https://doi.org/10.1007/s11707-017-0646-z

121. Zhang F, Biederman JA, Dannenberg MP, Yan D, Reed SC, Smith WK. Five decades of observed daily precipitation reveal longer and more variable drought events across much of the Western United States. Geophys Res Lett. 2021; 48: e2020GL092293. https://doi.org/10.1029/2020GL092293

122. Rhodes CJ. Pollinator decline–an ecological calamity in the making? Sci Prog. 2018; 101: 121–160. https://doi.org/10.3184/003685018X15202512854527 PMID: 29669627

123. Montgomery GA, Dunn RR, Fox R, Jongejans E, Leather SR, Saunders ME, et al. Is the insect apoca-lypse upon us? How to find out. Biol Conserv. 2020; 241: 108327. https://doi.org/10.1016/j.biocon.2019.108327

124. Pinkert S, Barve V, Guralnick R, Jetz W. Global geographical and latitudinal variation in butterfly spe-cies richness captured through a comprehensive country-level occurrence database. Glob Ecol Bio-geogr. 2022; 31: 830–839. https://doi.org/10.1111/geb.13475

125. Souther S, Randall V, Lyndon N. The use of citizen science to achieve multivariate management goals on public lands. Diversity. 2021; 13: 293. https://doi.org/10.3390/d13070293

126. Alkemade R, Reid RS, Berg M van den, Leeuw J de, Jeuken M. Assessing the impacts of livestock production on biodiversity in rangeland ecosystems. Proc Natl Acad Sci. 2013; 110: 20900–20905. https://doi.org/10.1073/pnas.1011013108 PMID: 22308313

127. Augustine D, Davidson A, Dickinson K, Van Pelt B. Thinking like a grassland: challenges and opportu-nities for biodiversity conservation in the Great Plains of North America. Rangel Ecol Manag. 2021; 78: 281–295. https://doi.org/10.1016/j.rama.2019.09.001

128. DiTomaso JM. Invasive weeds in rangelands: Species, impacts, and management. Weed Sci. 2000; 48: 255–265. https://doi.org/10.1614/0043-1745(2000)048[0255:IWIRSI]2.0.CO;2

129. Safford H, Hudson M. Review of fire management in the American West, HudsonMark. Nat Areas J. 2015; 35: 491–493.

130. Hudson M. Fire management in the American West: forest politics and the rise of megafires. Univer-sity Press of Colorado; 2011.

131. Fan Y. Understanding US drought in past 120+ years. Clim Predict ST Dig.: 116.

132. Barton K, Shiels A. Additive and non-additive responses of seedlings to simulated herbivory and drought. USDA Natl Wildl Res Cent—Staff Publ. 2020. Available: https://digitalcommons.unl.edu/icwdm_usdanwrc/2374

133. Benson RD. Federal water law and the "double whammy": How the Bureau of Reclamation can help the West adapt to drought and climate change. Ecol Law Q. 2012; 39: 1049–1083.

134. Bernstein EJ, Albano CM, Sisk TD, Crews TE, Rosenstock S. Establishing cool-season grasses on a degraded arid rangeland of the Colorado Plateau. Restor Ecol. 2014; 22: 57–64. https://doi.org/10.1111/rec.12023

135. Woinarski JCZ, Fisher A. Conservation and the maintenance of biodiversity in the rangelands. Rangel J. 2003; 25: 157–171. https://doi.org/10.1071/rj03013

136. Bonilla-Moheno M, Aide TM. Beyond deforestation: Land cover transitions in Mexico. Agric Syst. 2020; 178: 102734. https://doi.org/10.1016/j.agsy.2019.102734

137. Alison J, Botham M, Maskell LC, Garbutt A, Seaton FM, Skates J, et al. Woodland, cropland and hedgerows promote pollinator abundance in intensive grassland landscapes, with saturating benefits of flower cover. J Appl Ecol. 2022; 59: 342–354.

138.   Bowers HM. Pollinator ecology, habitat management, and landscape restoration on federal and private lands in South-East Washington State. Washington State University; 2018.

139.   McCormick ML, Aslan CE, Chaudhry TA, Potter KA. Benefits and limitations of isolated floral patches in a pollinator restoration project in Arizona. Restor Ecol. 2019; 27: 1282–1290.

140.   Cutlip K. Pollinator gardens and generated insect activity. Proc W Va Acad Sci. 2019;91.

141.   Glenny W, Runyon J, Burkle L. Assessing pollinator friendliness of plants and designing mixes to restore habitat for bees. Gen Tech Rep RMRS-GTR-429 Fort Collins CO US Dep Agric For Serv Rocky Mt Res Stn 54 P Httpsdoi Org102737RMRS-GTR-429. 2022; 429.

142.   Glenny W, Runyon JB, Burkle LA. A review of management actions on insect pollinators on public lands in the United States. Biodivers Conserv. 2022; 1–22.

143.   Kearney J. Pollinator communities on public lands: creating new opportunities for management. PhD Thesis. 2020.

144.   Kahal N, Kinas H. Management for pollinator habitat in Alberta. 2021.

145.   Broadhurst LM, Jones TA, Smith FS, North T, Guja L. Maximizing seed resources for restoration in an uncertain future. BioScience. 2016; 66: 73–79. https://doi.org/10.1093/biosci/biv155

146.   Greene SL, Carver D, Khoury CK, Irish BM, Olwell P, Prescott L. Seeds of success: Collateral benefits to agricultural crop improvement, research, and education. Crop Sci. 2019; 59: 2429–2442.

147.   Ladouceur E, Jiménez-Alfaro B, Marin M, Vitis MD, Abbandonato H, Iannetta PPM, et al. Native seed supply and the restoration species pool. Conserv Lett. 2018; 11: e12381. https://doi.org/10.1111/conl.12381 PMID: 29937920

148.   Baldock KC. Opportunities and threats for pollinator conservation in global towns and cities. Curr Opin Insect Sci. 2020; 38: 63–71. https://doi.org/10.1016/j.cois.2020.01.006 PMID: 32126514

149.   Wenzel A, Grass I, Belavadi VV, Tscharntke T. How urbanization is driving pollinator diversity and pollination–A systematic review. Biol Conserv. 2020; 241: 108321. https://doi.org/10.1016/j.biocon.2019.108321

150.   Theodorou P, Radzevičiūtė R, Lentendu G, Kahnt B, Husemann M, Bleidorn C, et al. Urban areas as hotspots for bees and pollination but not a panacea for all insects. Nat Commun. 2020; 11: 576. https://doi.org/10.1038/s41467-020-14496-6 PMID: 31996690

151.   Shirey V, Belitz MW, Barve V, Guralnick R. A complete inventory of North American butterfly occurrence data: narrowing data gaps, but increasing bias. Ecography. 2021; 44: 537–547. https://doi.org/10.1111/ecog.05396