

Partitioning interaction turnover among alpine pollination networks: spatial, temporal, and environmental patterns

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Abstract. Ecologists have taken two distinct approaches in studying the distribution and diversity of communities: a species-centric focus and an interaction-network based approach. A current frontier in community-level studies is the integration of these perspectives by investigating both simultaneously; one method for achieving this is evaluating the relative contributions of species turnover and host switching towards interaction turnover (i.e., the dissimilarity in interactions between two networks). We performed observations of plant-pollinator interactions to investigate (1) patterns in interaction turnover across spatial, temporal, and environmental gradients and (2) the relative contribution of pollinator species turnover, floral turnover, simultaneous pollinator & floral turnover, and host switching towards interaction turnover. Field work was conducted on the Beartooth Plateau, an alpine ecosystem in Montana and Wyoming, with weekly observations of plant-pollinator interactions across one growing season. Interaction turnover increased through time, with magnitudes consistently greater than 80%, even at time intervals as short as one week. Floral species turnover (41%) and simultaneous floral and pollinator species turnover (36%) accounted for almost all interaction turnover while host switching accounted for only 5%. Interaction turnover also significantly increased with spatial and elevational distance, albeit with lesser magnitudes than with temporal distance. The marginal spatial pattern was present for only some taxa (*Bombus* spp. and solitary bee species), potentially indicating variable habitat use by pollinators across the landscape. Weak environmental trends may be a consequence of unmeasured environmental variables, yet our finding that environmental gradients structure plant-pollinator interaction partitions had not previously been tested with empirical data. Our observations suggest that host switching does not readily occur at the scales of alpine flowering phenology (i.e., ~1 week); however, whether lack of host switching is indicative of inflexible pollinator foraging, or, more likely, a lack of opportunity or necessity to switch hosts, requires further investigation.

Key words: beta diversity; elevation; spatiotemporal.

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INTRODUCTION

One of the foundational goals in community ecology is to understand patterns of diversity and distributions of species across environmen-

tally heterogeneous landscapes (Hutchinson 1953) and how those patterns change through time (Levin 1992). Community ecologists have taken two distinct approaches in assessing these patterns: a species-centric focus and a network-

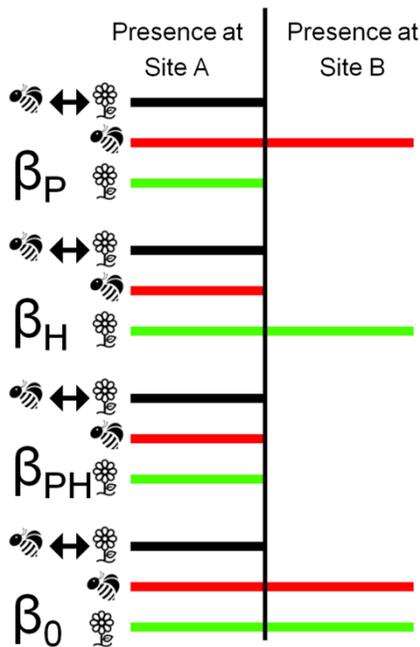


Fig. 1. Possible explanations for turnover of a single plant-pollinator interaction from one sampling site to another; the interaction is represented in black, pollinator species in red, and plant species in green. β_P : interaction turnover due to the turnover of the plant species while the pollinator persists, β_H : interaction turnover due to the turnover of the pollinator species while the plant persists, β_{PH} : interaction turnover because both the plant and pollinator species turnover, or β_0 : both species persist, but the interaction still turns over (i.e., host switching). Bee icon designed by Wei Zhang and flower icon designed by Danilo Gusmão Silveira from The Noun Project.

based focus on the interactions between species (Tylianakis et al. 2008). The species focused approach frequently assesses compositional changes in ecological communities to determine conditions necessary for conservation (Legendre et al. 2005, Cumming et al. 2010). These compositional changes are often measured with species turnover, the directional dissimilarity in species identity and abundance across spatial, temporal or environmental gradients (Anderson et al. 2011). By contrast, the ecological network approach typically investigates the structural dynamics of species interaction networks to explore community structure, function, or ecological processes like pollination (Dyer et al.

2010, Poisot et al. 2012).

A current frontier in community-level studies of ecological systems is the integration of the species and interaction network focused perspectives by investigating both simultaneously; this can be achieved by evaluating the contribution of species turnover to interaction turnover (i.e., the dissimilarity in interaction identity between two networks; Novotny 2009, Poisot et al. 2012). Given that we can document shifts in interactions across spatial, temporal, or environmental gradients to assess their importance in structuring interaction dynamics (e.g., Burkle and Alarcón 2011), interaction turnover is conceptually similar to species turnover, in that we can use community-level tools and metrics to analyze interactions between species (e.g., Blüthgen et al. 2008). In addition to the contribution of species turnover to interaction turnover, interaction turnover can also occur due to host switching, in which foraging preferences of one trophic level differ between two communities that overlap in species composition. For instance, host switching occurs when you have a pair of species that are present in two networks, yet that pair only interacts in one of the two networks (Fig. 1, Novotny 2009). These “partitions” of interaction turnover (i.e., due to species turnover versus host switching) additively comprise the interaction turnover between two networks (Novotny 2009, Poisot et al. 2012). This framework can elucidate how the species diversity of communities is structured across spatiotemporal and environmental gradients while simultaneously providing mechanistic explanation for how community composition and species behavior contribute to the structure of ecological interaction networks. Typically, species turnover is measured across spatial or environmental gradients for the purposes of determining species distributions (e.g., Kraft et al. 2011) or from year-to-year to assess species’ presence on the landscape (e.g., Olesen et al. 2011). When considering *interaction* turnover within one season, however, there is an inherent contribution from phenophases; therefore, the species turnover and host switching components of interaction turnover are not directly equivalent to “traditional” species turnover (see Whittaker 1960), as they incorporate phenological aspects of important life-history events (e.g., flowering periods of plants, flight periods of pollinators,

etc.). Therefore, throughout this paper our measures of turnover include species' phenologies and do not perfectly reflect "true" species turnover.

Given that pollination is an essential ecosystem service (De Groot et al. 2002, Klein et al. 2007), pollination networks (i.e., webs describing interactions between plants and their pollinating partners) provide an ideal system in which to test hypotheses concerning species and interaction turnover across ecologically meaningful gradients. Traditional investigations of plant communities have shown that plant species typically have nonrandom distributions through space at the spatial scale at which plant-pollinator networks are often quantified ($<10^6$ m²; Kissling et al. 2012) and are structured largely by microhabitat gradients, temperature, and precipitation (Kikvidze et al. 2005). Likewise, pollinator species have a high degree of spatial, temporal, and environmental turnover (Minckley et al. 1999, Devoto et al. 2009). The interaction network approach to studying plant-pollinator communities has provided evidence of extremely high variability in plant-pollinator interactions between years (Petanidou et al. 2008, Olesen et al. 2011), with interannual interaction persistence ranging from 1.4–22% (Dupont et al. 2009, Fang and Huang 2012). At finer time scales, there is some evidence that pollinators exhibit host switching on a diurnal basis (Baldock et al. 2011), yet the degree to which pollinators are flexible in their interactions at other temporal scales relevant for flowering plant phenophases (i.e., 1–2 weeks; Burkle and Alarcón 2011, Burkle et al. 2013) is unknown. Only one study has examined interaction turnover across spatial and environmental gradients, finding an increase in interaction turnover with increasing environmental distance but no significant pattern of interaction turnover across a geographic distance of 3 km (Burkle and Alarcón 2011).

In the few studies that have considered turnover in plant-pollinator interactions, each gradient was tested in isolation, and the relative effects of spatial, temporal, or environmental distances on interaction turnover have not yet been assessed for pollination networks. We expect the temporal gradient to be a strong contributor towards interaction turnover, as pollination is primarily a phenological process

(Encinas-Viso et al. 2012). Additionally, environmental heterogeneity across landscapes likely contributes to interaction turnover via its role in structuring plant communities (Kikvidze et al. 2005) as well as via patchy nesting habitat distributions for different pollinator species (Jauker et al. 2009). While interaction turnover among plant-pollinator networks has been shown to exhibit strong spatial patterns at local scales, it remains possible for interaction turnover to be structured by greater spatial extents than previously studied (Burkle and Alarcón 2011). Furthermore, there may be patterns in interaction turnover that only emerge through partitioning the contributions of species turnover and host switching. For instance, even if interaction turnover appears unrelated to spatial distances, it remains possible that the contribution of species turnover increases across space while the degree of host switching declines.

The relative contribution of species turnover and host switching to interaction turnover among pollination networks has only been assessed between (not within) seasons. In the few cases where interaction turnover has been partitioned using this approach, the contribution of species turnover was found to be highly variable, ranging from 20% to 70% interannually (Petanidou et al. 2008, Olesen et al. 2011). For increasing temporal distances within a growing season, we expect the contribution of species turnover to increase due to species-specific phenophases for both flowering plants and pollinators, influencing the composition of species assemblages actively involved in the pollination network (Encinas-Viso et al. 2012). The degree of host switching is likely driven by differences in relative floral abundances or shifts in intra- and inter-specific competition for floral resources that vary across environmental gradients (e.g., Hoiss et al. 2012).

To address these critical gaps in understanding the contribution of species turnover and host switching towards interaction turnover across spatiotemporal and environmental gradients, we investigated pollination networks across spatial, temporal, and environmental (i.e., elevation, slope, and between aspects) gradients in an alpine meadow ecosystem. Using observations of plant-pollinator interactions through one growing season, we asked: (1) what are the

patterns in interaction turnover across spatial, temporal, and environmental gradients, and (2) within these patterns, what is the relative contribution of species turnover vs. host switching to interaction turnover?

METHODS

Study site

Field work was conducted after snowmelt during the summer season in the alpine tundra of the Beartooth Plateau located in the Custer and Shoshone National Forests of Carbon County, Montana and Park County, Wyoming, centered approximately at 45°00' N 109°25' W. The Plateau covers an area of approximately 186 km², the majority of which is above 3000 m in elevation (Pattie and Verbeek 1966). Thus, the growing season is short, averaging 80 days long with a mean daily temperature of 8°C (Billings 1973). The area's vegetation is dominated by *Geum rossii*, *Deschampsia* spp., *Carex* spp., *Salix* spp., and several different cushion plants (e.g., *Silene acaulis* and *Trifolium nanum*) (Johnson and Billings 1962). We selected 16 study meadows based on slope, elevation, and aspect (Appendix: Table A1). Study meadows were separated by a minimum of 400 meters to reduce the likelihood of individual pollinators moving between sampling sites. Field site selection took place in early summer (June 12–14, 2012) of a single growing season and only meadows which were free of snow by that time were used for this study. This was done for the purpose of keeping unmeasured environmental variability, such as soil moisture, to a minimum. Given the focus of our study questions on intra-annual variation in interactions, one field season is sufficient; however, this study design cannot assess whether spatial or environmental patterns of turnover are consistent from year to year. Elevation of study meadows ranged from 2975 to 3310 m, and slope varied from 1.6° to 17.7° (ArcMap 10 [ESRI 2011] using the National Elevation Dataset available from the U.S. Geological Survey; Gesch et al. 2002, Gesch 2007). Of the 16 meadows, nine were southwest facing slopes and seven were northeast facing.

Field methods

Plant-pollinator interactions.—Fifteen minutes

were spent observing a semi-circular area of every plant species present in each of the 16 meadows once per week throughout the flowering season (nine weeks; June 20–August 21, 2012) and hand netting all observed pollinators. This method was selected over transect-based methods of sampling pollinators because it provides an even distribution of sampling effort across all flowering species present (Gibson et al. 2011), and thus it provided the best opportunity for observing rare pollinator species and the entire range of unique pairings within these pollination networks. Additionally, this sampling method allowed us to compare many networks that were sampled with the same intensity, while minimizing concern over sampling all existing interactions across networks. Pollinators were defined as only those floral visitors which came into contact with the reproductive parts of the flower. Multiple (typically >20) flowering plants of a species were observed during each observation period; this was not always possible for rare species. The time of day (AM or PM) for sampling each study meadow was randomized by week, and all pollinator observations were done only during clear, calm weather from 0800 to 1700. *Bombus* queens were identified to species in the field and released. All other pollinators were identified in the lab under dissecting microscopy to the lowest taxonomic resolution possible. When species identity could not be determined, samples were classified into morphospecies and kept consistent between all meadows and across the entire season. These pollinator observations were used to create presence/absence plant-pollinator interaction matrices for each sampling event at each meadow.

Floral community.—We marked a 50 × 2 m band transect at each meadow for the purpose of quantifying the plant community and potential floral resources across the course of the season. Each transect was observed weekly, in conjunction with pollination sampling, and the number of open flower heads per species was recorded. Any plant species flowering in the meadow that did not fall within the transect were recorded as singletons.

Analyses

To assess how the plant and pollinator communities varied across spatial, temporal,

and environmental gradients, we calculated Whittaker's beta diversity ($\beta_w = S/\alpha - 1$, where S is the total number of species across sites and α is the average number of species per site) of plants and pollinators using the 'vegan' package for R (Oksanen et al. 2012); thus, this index uses binary (presence/absence) data. Turnover was calculated between all possible pairwise combinations of site and week. To determine plant species turnover most relevant to pollination, we calculated plant species turnover from the floral community transect data (i.e., the number of open flower heads of each species) and thus plant species turnover is a measure of floral turnover. Floral and pollinator species turnover were then separately compared to the spatial, temporal, and environmental gradients using multiple regressions of distance matrices (MRM) for distance, time, slope, and elevation, as well as Welch's t-test to compare aspects.

Interaction turnover (i.e., dissimilarity between pair wise combinations of sites and weeks) was computed as

$$\beta_{cc} = b + c/a + b + c$$

where a is the number of interactions shared between two networks, " b " is the number present only in the first network, and " c " is the number present only in the second. This measure was selected for two reasons: (1) it is a "broad-sense" measure of beta diversity, in that it incorporates differences in interaction composition in regards to richness changes, whereas a narrow-sense measure (e.g., Simpson's index) would ignore differences in interaction richness between networks (Koleff et al. 2003) and (2) it can easily be partitioned into additive components that allow us to discern the cause of an interaction's turnover (Novotny 2009):

$$\beta_{cc} = \beta_{PH} + \beta_P + \beta_H + \beta_0.$$

The subscript "P" represents plants, whereas "H" denotes the higher trophic level (i.e., pollinators). β_{cc} interaction turnover between two networks, is made up of four additive partitions: β_P the proportion of interaction turnover due to plant species turnover; β_H , the proportion due to pollinator species turnover; β_{PH} , the proportion due to simultaneous turnover of both the floral and pollinator species involved in an interaction; and β_0 , the proportion

due to host-switching (i.e., when both partners in an interaction are present in two networks but only interact in one).

Utilizing the hand-netting data, plant-pollinator interaction networks were constructed for every possible pairwise combination of study meadow ($n = 16$) and week ($n = 9$), resulting in a total of 144 quantitative plant-pollinator interaction matrices. We then calculated β_{cc} , β_P , β_H , β_{PH} , and β_0 for every pairwise combination of these interaction matrices using modified 'betalink' (Poisot et al. 2012) R script (see Appendices B and C). Additionally, matrices were also created for all possible pairwise combinations of (1) spatial distance between sites, (2) temporal distance between sampling events at all meadows, (3) elevational difference between meadows, (4) difference in slope between meadows, and (5) dissimilarity in aspect between meadows. Relationships between interaction turnover (β_{cc} and each of the four partitions) and spatial distance, temporal distance, elevational difference, difference in slope, and difference in aspect were tested using MRM within the R package 'ecodist' (Goslee and Urban 2007). MRM vectorizes the matrices used and compares a single response matrix (i.e., the interaction turnover partitions) against multiple matrices of explanatory variables. It differs from a standard regression through its significance testing; MRM performs permutations on the response matrix while holding explanatory matrices constant. For the purposes of our study, MRM allowed us to compare multiple distance matrices of different units, while being more robust than similar multiple-matrix methods (Legendre et al. 1994, Lichstein 2007). To determine if observed patterns in interaction turnover (see *Results*) were driven by certain taxa, analyses were repeated for separate taxonomic groupings of pollinators: (1) solitary bees (mostly *Lassioglossum* spp. and *Osmia* spp.), (2) *Bombus* spp., (3) Syrphidae and Bombyliidae (i.e., obligate nectar or pollen foraging Diptera), (4) all other Diptera, and (5) Lepidoptera. Finally, we performed sampling completeness analyses utilizing the Chao estimator (Chao et al. 2009; Appendix) All analyses were performed in R (R Core Team 2013).

RESULTS

Over 282 hours, 126 pollinator morphospecies were observed on 55 plant species (Appendices D and E). We observed 989 interactions, with 404 of those representing unique plant-pollinator interactions. Both plant and pollinator species turnover increased significantly but minutely across spatial distance, time, and elevational difference. There was no species turnover between aspects or across slope (Fig. 2 and Table 1).

Mean total interaction turnover between sampling events was greater than 90% (0.929, 95% CI: 0.927–0.931), the majority of which was driven by the turnover of the floral community (mean $\beta_P = 0.412$, 95% CI: 0.408–0.417). Simultaneous plant and pollinator turnover was the next largest contributor at 36.3% (95% CI: 0.358–0.369), while interaction turnover due from pollinators ($\beta_H = 0.099$, 95% CI: 0.097–0.102) and host switching ($\beta_0 = 0.054$, 95% CI: 0.052–0.055) contributed relatively little to total interaction turnover. All partitions of interaction turnover varied significantly with increasing temporal distance: β_{CC} , β_{PH} , and β_P increased by 2%, 4%, and 2% per week, respectively, while β_H and β_0 declined 2% and 1% per week (Table 2, Fig. 3). Interaction turnover partitions followed similar patterns, albeit with much lower rates of change across elevation (c. 3% total increase across the entire elevational range for β_{CC}), with the exception of β_P , which did not vary with elevation (Table 2, Fig. 3). β_{CC} and β_H increased c. 1.6% and 2.5%, respectively, across the entire spatial distance of 8 km. β_0 was 0.7% greater on southwest aspects (0.066) compared to northeast aspects (0.044) (Table 2, Fig. 3). There were no observed relationships between slope and any interaction turnover partition (Table 2, Fig. 3). When analyses were repeated using taxonomic groupings of pollinators instead of morphospecies, we observed the same patterns (Appendix: Tables A2–A6), except that only solitary bees and *Bombus* spp. showed significant increases in interaction turnover across spatial distance (β_{CC} increased c. 2.2% for *Bombus* spp., β_H increased c. 1.1% for both *Bombus* spp. and solitary bees across the entire spatial range of 8 km; Tables A2 and A3).

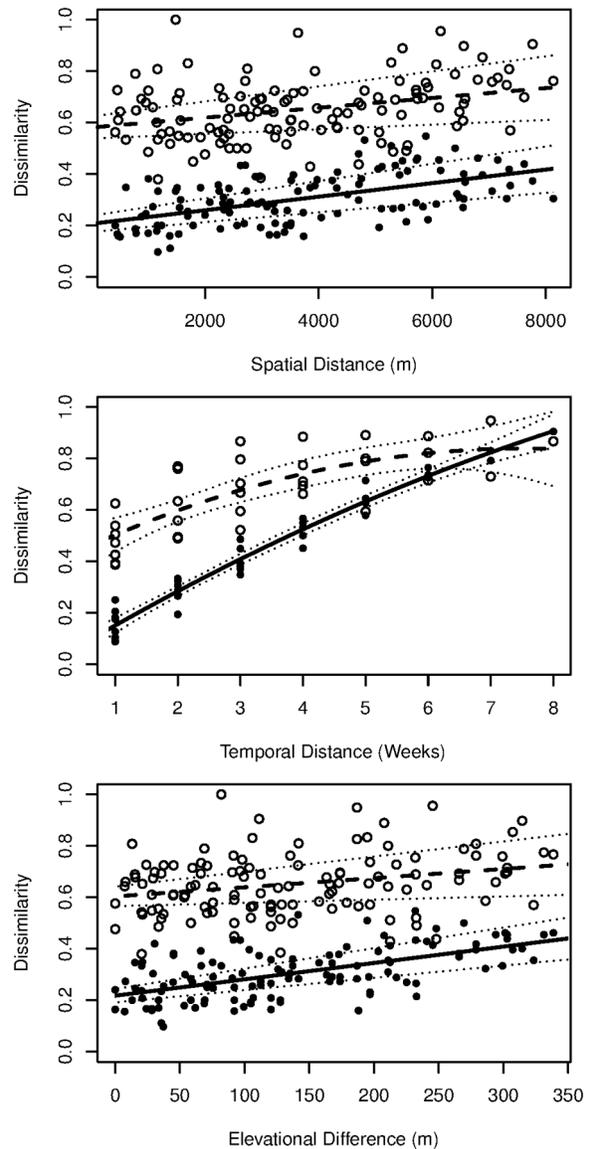


Fig. 2. Species turnover for pollinators (open circles, dashed lines) and flowering plants (filled circles, solid lines) across spatial distance, time, and elevation. The y-axis for each plot is Whittaker's beta diversity. Pollinators and plants both show significant turnover across space, through time, and across elevation, yet pollinator turnover is consistently higher than floral turnover. Multiple Matrix Regressions all have p-values of <0.01 , and dotted lines represent 95% confidence intervals. See Table 1 for statistical summary.

Table 1. Pollinator and floral turnover compared against spatial, temporal, and environmental variables using Multiple Matrix Regression for spatial distance, time, elevation, and slope. Aspect differences were tested using Welch's t-test. The p-values that are <0.05 appear in boldface.

Turnover	Spatial distance			Time			Elevation			Slope			Aspect		
	R ²	Estimate	p	R ²	Estimate	p	R ²	Estimate	p	R ²	Estimate	p	Mean NE	Mean SW	p
Pollinator	0.100	1.92e-05	0.005	0.540	0.057	0.001	0.074	3.57e-04	0.014	-0.003	-0.002	0.734	0.668	0.634	0.116
Floral	0.298	2.63e-05	0.001	0.956	0.011	0.001	0.347	6.36e-04	0.001	-4.77e-06	-6.79e-05	0.983	0.302	0.306	0.827

DISCUSSION

The turnover of plant-pollinator interactions within one growing season was primarily a temporal process in alpine networks. Environmental factors (i.e., elevation and aspect) were also significant determinants of interaction turnover, yet with a less pronounced pattern than time. Increasing spatial distance among study meadows marginally influenced interaction turn-

Table 2. Interaction turnover partitions across abiotic gradients as tested by Multiple Matrix Regressions. F stat and R² for each full model are below their respective β . The p-values that are <0.05 appear in boldface. P-values for all full models were <0.001 with $F_{5,10290}$.

Turnover partition	F	R ²	Variables	Estimate	p
β_{cc}	585.0	0.22	Spatial distance	2.08e-06	0.048
			Time	2.25e-02	0.001
			Elevation	1.04e-04	0.001
			Slope	5.71e-04	0.400
			Aspect	2.23e-03	0.225
β_{PH}	199.5	0.09	Spatial distance	-1.98e-06	0.740
			Time	3.85e-02	0.001
			Elevation	2.95e-04	0.037
			Slope	1.09e-04	0.971
			Aspect	7.92e-03	0.290
β_P	74.5	0.03	Spatial distance	2.07e-06	0.677
			Time	2.00e-02	0.001
			Elevation	7.89e-05	0.547
			Slope	-1.57e-03	0.659
			Aspect	5.35e-03	0.403
β_H	436.0	0.17	Spatial distance	3.21e-06	0.057
			Time	-2.15e-02	0.001
			Elevation	-1.94e-04	0.001
			Slope	8.82e-04	0.452
			Aspect	-3.82e-03	0.120
β_0	464.1	0.18	Spatial distance	-1.22e-06	0.222
			Time	-1.45e-02	0.001
			Elevation	-7.58e-05	0.004
			Slope	1.15e-03	0.115
			Aspect	-7.22e-03	0.001

over, however, this pattern was only observed for certain pollinator taxa (i.e., solitary bees and *Bombus* spp.). The contribution of floral turnover and, to a lesser degree, the contribution of simultaneous floral and pollinator turnover comprised the majority of interaction turnover, while host switching was not an important contributor to interaction turnover among these networks. With these results, we begin to integrate the species- and network-centric perspectives in community ecology by demonstrating the role of abiotic gradients in structuring species and their interactions. Furthermore, by simultaneously assessing the partitioning of interaction turnover across space, time, and environment, we have begun to elucidate the gradients (i.e., time and environment) and scales (i.e., landscape-level) most relevant for conservation of plant-pollinator interaction networks in this system.

Interaction turnover was primarily driven by phenological changes in plant species over the growing season. For pollination, a phenologically structured process (Encinas-Viso et al. 2012), to exhibit strong temporal patterns is no surprise. The magnitude of change was immense at fine time scales, where interaction turnover among networks was consistently greater than 80% over time spans as short as one week. This extremely rapid interaction turnover could be evidence of the instability of plant-pollinator networks with short flowering seasons (Encinas-Viso et al. 2012). Rapid interaction turnover could also be a mechanism for ensuring pollination and fruiting success in a harsh alpine system by minimizing phenological overlap over evolutionary time-scales. A high degree of phenological overlap of many flowering species within a community has been found to be negatively

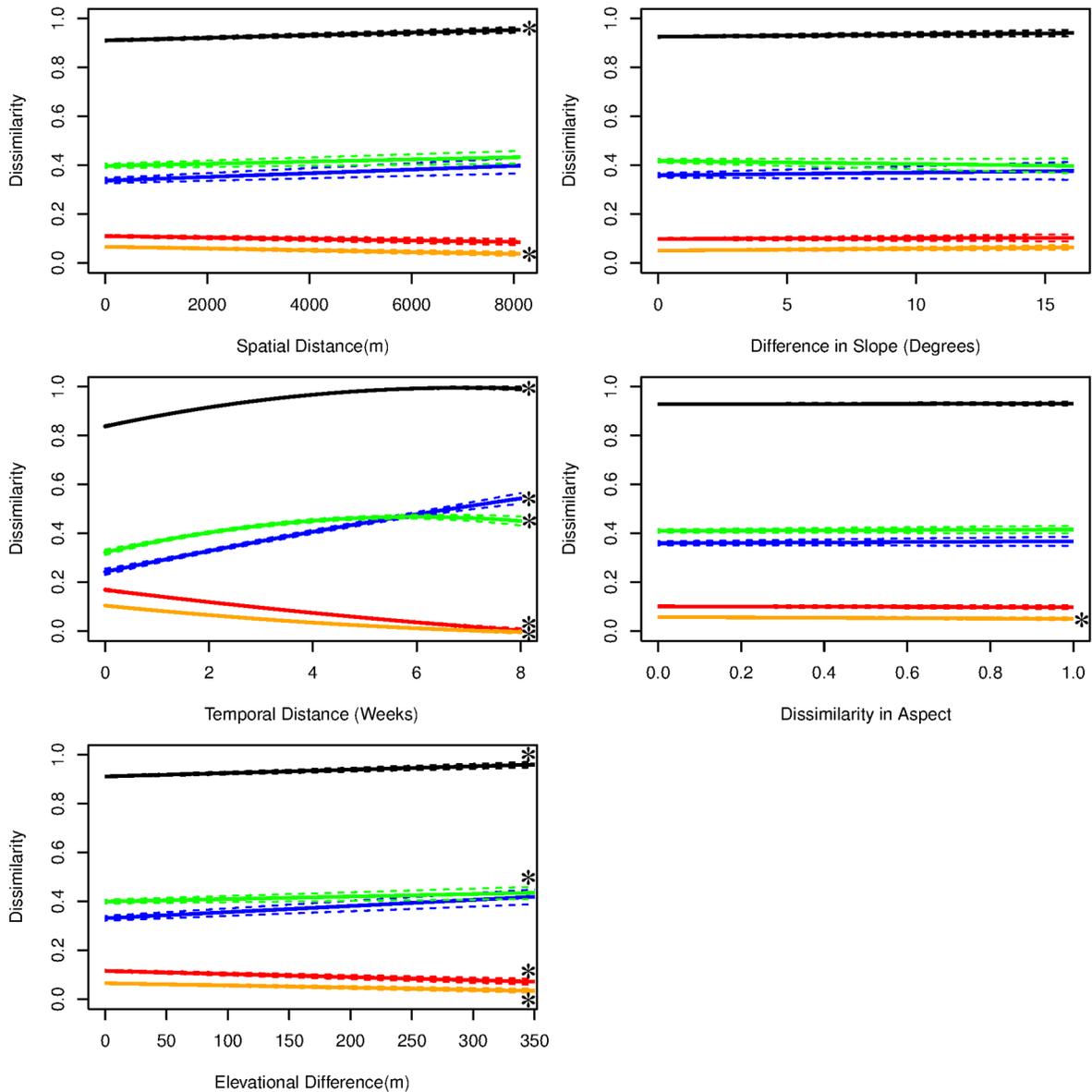


Fig. 3. Interaction turnover partitions across abiotic gradients. Black = β_{cc} , blue = β_{PH} , green = β_B , red = β_H , and orange = β_0 . Dashed lines represent 95% confidence intervals, and an asterisk represents a significant Multiple regression on distance matrices (MRM) test (i.e., p -value < 0.05). Interaction turnover significantly changed with distance, time, and elevation. Magnitude of change was greatest through time. Spatial patterns were only present for *Bombus* spp. and solitary bees (see Appendix: Tables A2 and A3).

associated with conspecific pollen transfer (Aizen and Rovere 2010). In our system it is possible that the rapid floral and interaction turnover may be a result of selection against overlapping flowering phenophases, which could help to ensure conspecific pollen transfer. Interestingly, we found

the magnitude of intra-annual interaction turnover to be similar to that of inter-annual interaction turnover in other systems. Inter-annually, 98.6% (Fang and Huang 2012) to 78% of interactions (Dupont et al. 2009) turn over between years. Similarly, we found an average

interaction turnover of 92.1% across one growing season. Therefore, interaction turnover among pollination networks through time is substantial both from year-to-year and within-season, yet the main mechanisms driving these patterns are different: interannual interaction turnover is driven by a combination of year-to-year variance in community composition and abundance and/or host switching (Petanidou et al. 2008, Dupont et al. 2009, Olesen et al. 2011), whereas intra-annual interaction turnover is dominated by species turnover via phenological processes. However, given that our study design was comprised of only one season of data, we were unable to assess if the high magnitude of interaction turnover is consistent across multiple years.

Given the low contribution of host switching towards interaction turnover in our study, host switching may be primarily an interannual property of pollinator foraging that does not frequently occur at the scales herein. Until now, the contribution of host switching to interaction turnover among pollination networks has only been reported twice, and in both cases it contributed significantly to interaction turnover between years: 81% in an arctic pollination network (Olesen et al. 2011) and 30% in a temperate Mediterranean system (Petanidou et al. 2008). By contrast, host switching comprised only 5% of interaction turnover in our intra-annual study. A potential mechanism for this discrepancy may be that generalist pollinator species, when observed within a single season, often demonstrate “apparent specialization”, the capacity to interact with many different plant species but doing so only across several years (Petanidou et al. 2008). Alternatively, we cannot exclude the possibility that our observed patterns may be system specific; host switching may contribute more strongly to within-season interaction turnover at lower elevations (i.e., non-alpine systems), due to an increase in inter- and intra-specific competition given higher abundance and diversity of pollinators with decreasing elevation (Hoiss et al. 2012). Additionally, whether our observed lack of host switching is indicative of inflexible pollinator foraging, or, more likely, a lack of necessity to switch hosts, requires further investigation. There is some evidence to suggest that pollinator preference, specialization, and

flexibility can be site-specific (Fründ et al. 2010), and therefore other systems may very well contain different patterns of host switching than those herein. However, pollinator behavior has not been found to change with different ecological conditions (Vamosi et al. 2014). Our weekly sampling cannot rule out the possibility that host switching may be more prevalent if investigated at finer temporal scales, such as daily or within a single day (e.g., Baldock et al. 2011), or that host switching may occur in some years and not others. Our results do, however, lend evidence to the idea that alpine pollinators do not readily switch hosts at the weekly scales important for flowering plant phenologies (Burkle and Alarcón 2011, Burkle et al. 2013).

Given that we found pollinator species turnover to be two-fold greater than floral turnover across space, time, and elevation, it is interesting that pollinators alone did not contribute more towards interaction turnover. The majority of interaction turnover among pollination networks was caused by floral turnover (41%) and simultaneous floral and pollinator turnover (36%), while pollinator species turnover alone accounted for only 10% of interaction turnover. This implies that the phenology of pollinators alone has relatively little effect on network structure, and that the floral community plays a primary role in driving interaction turnover (cf. Potts et al. 2003, Encinas-Viso et al. 2012). The key is that while plant turnover may be low, the effects of plant turnover are massive; this means that while plants may turn over slowly, they make substantial changes to the interaction network when they do turn over. Mechanistically, pollinator phenologies in our system may have experienced selection to respond to environmental cues which coincide with the phenophases of their preferred foraging plants. This sort of selection could then explain the combination of a high contribution of simultaneous floral-pollinator turnover with low contribution of pollinator turnover. The contribution of plant vs. pollinator turnover to interaction turnover had not previously been assessed, and thus additional research in other, non-alpine ecosystems is required to determine the generality of our observed patterns.

Environmental gradients have been found to structure plant-pollinator interactions (Arroyo et al. 1985, Burkle and Alarcón 2011). Similarly, we

found elevation and aspect to be significant determinants of interaction turnover. However, contrary to expectations, the magnitude of interaction turnover due to environment was minimal, with only a 3% increase in interaction turnover across the entire elevational range. Because plants at higher elevations tend to have delayed and truncated flowering phenologies compared to lower elevations, we hypothesized that elevational differences between study meadows would result in interaction turnover, especially early in the summer when high-elevation meadows had just begun flowering (e.g., Pyke et al. 2011). However, these shifts in floral phenology with elevation were not strong enough to drive interaction turnover. Instead, the effects of elevation on interaction turnover were likely driven by some other unmeasured environmental factor strongly correlated with elevation. For instance, while all study meadows were snow-free when data collection began, we cannot be certain of exact snowmelt dates, which can be very important in determining alpine flowering phenophase (Billings and Mooney 1968). Aspect significantly, but minimally, affected the host switching component of interaction turnover, again likely representing unmeasured environmental variation with the potential to affect pollinator foraging (e.g., temperature, shade, soil moisture).

Interaction turnover was weakly structured by geographic space at the scale utilized for this study (ca. 1.6×10^7 m²). Although models indicate that mutualistic interactions have the potential to demonstrate strong spatial structuring (Kissling et al. 2012), no significant trend, positive or negative, until now had been found for plant-pollinator interaction turnover across space (Burkle and Alarcón 2011). However, the rate of change in total interaction turnover was minimal (1.6%) across the spatial range of our study. The weak spatial signal could result from pollinator taxa operating at different spatial scales, as we only found a spatial relationship with interaction turnover for solitary bee species and *Bombus* spp. Bee species, both social and solitary, often have vastly different average foraging ranges (Gathmann and Tscharrnke 2002) as well as more specific habitat requirements than other pollinators (e.g., Diptera) (Jauker et al. 2009). Thus, patchily distributed areas of quality nesting habitat for bees across

our study area may contribute to our observed patterns in interaction turnover across geographic space. Furthermore, while we accounted for spatial autocorrelation of three major environmental gradients (i.e., elevation, slope, or aspect), the spatial arrangement of bee habitat may be related to unmeasured factors (e.g., soil moisture). Alternatively, it could be the amount of change in interaction turnover may be greater at larger spatial extents of study.

Through this study, we gained a better understanding of the relative contribution of species turnover and host switching to interaction turnover in pollination networks. Within a single growing season, interaction turnover was primarily driven by turnover of the floral community, and host switching was not a major contributor at the scales we considered. This information may be applied to help assess how community function will respond to anthropogenic disturbance. For example, an interaction network demonstrating a low degree of host switching at short time scales may, hypothetically, lack flexibility in its interaction structure and therefore may be more vulnerable to disturbance than a network which demonstrates relatively high host switching at the same temporal scales. Additionally, we are beginning to understand the relative importance of different abiotic gradients for interaction turnover, which may help predict the relevant land area, phenological processes, or specific ecosystem conditions necessary for conservation. In this study, we found that phenological processes within a growing season as well as environmental gradients structure plant-pollinator interactions. Thus, a management plan for this area may consider prioritizing (1) mitigation of factors affecting flowering phenology, such as anthropogenic climate change and (2) preservation of environmental heterogeneity across the Beartooth Plateau to conserve biodiversity and interaction diversity. Landscape heterogeneity could be maintained by minimizing future construction for tourism on unique environmental sites or active remediation of old mining sites (see Chambers et al. 1987, Chambers et al. 1990). Given that anthropogenic climate change and discrete disturbances (e.g., fire, flood) do not typically act at the same spatial, temporal, or environmental scales, assessing community function across multiple abiotic gradients simulta-

neously, such as in this study, can assist in predicting the responses of plant-pollinator interaction networks to different disturbances.

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SUPPLEMENTAL MATERIAL

APPENDIX

Sampling completeness

Sampling completeness for plant-pollinator interactions was tested using the Chao estimator (Chao et al. 2009) by calculating the estimated pollinator richness as observations of floral species were added. We also tested for under-sampling of all individual floral species by using the Chao estimator to assess if the estimated number of interactions was reached for each species. Additionally, we calculated the number of additional observations that would have been required to obtain 80%, 90%, and 99% of estimated species following methods from Chao et al. (2009). These analyses were performed in R using the ‘vegan’ package (Oksanen et al. 2012, R Core Team 2013).

Sampling completeness for pollinators was estimated to be 55% (126 observed, 228.4 estimated, see Fig. A1). We calculated that 1,901 observations would be needed to reach 80% completeness, 3,272 observations for 90%, and 7,827 for 99%. For plant species we found 3

species at 0–24% completeness, 8 at 25–49%, 7 at 50–74%, and 27 at 75–100% (see Supplement for individual species results).

Sampling for richness at either the species or interaction level is inherently problematic (Chao et al. 2009, Chacoff et al. 2012), yet our sampling completeness indicated that our results were not dramatically affected by our sampling methodology. Additionally, our sampling completeness of 55% is in line with similar recent studies (e.g., Chacoff et al. 2012, Devoto et al. 2012). Our phytocentric sampling approach may have contributed towards this value, since we likely sampled common pollinators more often than rare ones. However, we selected methods best suited for sampling the greatest possible number of unique links in a network (Gibson et al. 2011), and a more pollinator centric approach would have made it difficult to address our main questions. We found that to reach 80% sampling completeness would have required a two-fold increase in sampling effort (1,901 pollinators collected from 989).

Table A1. Elevation, aspect, and slope measured for each of the study meadows.

Site	Elevation (m)	Aspect	Slope (°)
1	3111	SW	11.8
2	3186	SW	7.8
3	3207	NE	11.5
4	3299	SW	17.8
5	3278	SW	6.1
6	3186	NE	7.6
7	3307	SW	7.8
8	3278	SW	9.7
9	3245	NE	12.6
10	3314	NE	1.7
11	2975	NE	6.8
12	3141	SW	10.8
13	3082	NE	9.5
14	3066	SW	10.2
15	3013	NE	13.7
16	3000	SW	5.6

Table A2. Interaction turnover partitions across abiotic gradients as tested by Multiple Matrix Regressions for solitary bee species. F stat and R^2 for each full model are below their respective β . The p-values that are <0.05 appear in boldface. $F_{5,10290}$ for all models.

Turnover partition	F	R^2	p	Variable	Estimate	p
β_{cc}	637.0	0.24	<0.001	Spatial distance	2.04e-06	0.142
				Time	3.25e-02	0.001
				Elevation	1.61e-04	0.001
				Slope	7.42e-04	0.408
				Aspect	3.99e-03	0.105
β_{PH}	84.8	0.04	0.003	Spatial distance	-7.52e-06	0.295
				Time	3.00e-02	0.001
				Elevation	2.75e-04	0.140
				Slope	-2.15e-03	0.701
				Aspect	9.31e-03	0.292
β_P	14.5	0.01	0.297	Spatial distance	6.98e-06	0.318
				Time	1.06e-02	0.031
				Elevation	-4.40e-05	0.788
				Slope	2.04e-03	0.679
				Aspect	2.35e-03	0.794
β_H	80.6	0.04	<0.001	Spatial distance	1.49e-06	0.016
				Time	-3.67e-03	0.001
				Elevation	-4.11e-05	0.005
				Slope	1.90e-04	0.654
				Aspect	-1.84e-03	0.070
β_0	96.8	0.04	<0.001	Spatial distance	1.09e-06	0.168
				Time	-4.43e-03	0.001
				Elevation	-2.90e-05	0.134
				Slope	6.66e-04	0.249
				Aspect	-5.84e-03	0.001

Table A3. Interaction turnover partitions across abiotic gradients as tested by Multiple Matrix Regressions for *Bombus* spp. F stat and R^2 for each full model are below their respective β . The p-values that are <0.05 appear in boldface. $F_{5,10290}$ for all models.

Turnover partition	F	R^2	p	Variable	Estimate	p
β_{cc}	626.5	0.23	<0.001	Spatial distance	2.77e-06	0.059
				Time	3.36e-02	0.001
				Elevation	1.12e-04	0.005
				Slope	7.69e-04	0.377
				Aspect	3.59e-03	0.187
β_{PH}	61.3	0.03	0.005	Spatial distance	-1.87e-06	0.808
				Time	2.66e-02	0.001
				Elevation	-7.61e-06	0.967
				Slope	-1.99e-03	0.724
				Aspect	1.41e-04	0.987
β_P	29.9	0.01	0.059	Spatial distance	3.33e-06	0.623
				Time	1.29e-02	0.013
				Elevation	1.98e-04	0.273
				Slope	3.00e-03	0.581
				Aspect	4.34e-03	0.640
β_H	113.8	0.05	<0.001	Spatial distance	1.39e-06	0.002
				Time	-3.12e-03	0.001
				Elevation	-5.10e-05	0.001
				Slope	-8.45e-05	0.757
				Aspect	-3.49e-04	0.604
β_0	93.1	0.04	0.04	Spatial distance	-8.38e-08	0.833
				Time	-2.72e-03	0.001
				Elevation	-2.75e-05	0.014
				Slope	-1.56e-04	0.584
				Aspect	-5.37e-04	0.427

Table A4. Interaction turnover partitions across abiotic gradients as tested by Multiple Matrix Regressions for Diptera of the family Syrphidae. F stat and R^2 for each full model are below their respective β . The p-values that are <0.05 appear in boldface. $F_{5,10290}$ for all models.

Turnover partition	F	R^2	p	Variable	Estimate	p
β_{cc}	650.4	0.24	<0.001	Spatial distance	2.19e-06	0.149
				Time	3.37e-02	0.001
				Elevation	1.34e-04	0.001
				Slope	4.51e-04	0.618
				Aspect	4.39e-03	0.114
β_{PH}	65.0	0.03	0.009	Spatial distance	-4.98e-06	0.502
				Time	2.70e-02	0.001
				Elevation	1.31e-04	0.482
				Slope	-3.07e-03	0.560
				Aspect	1.94e-03	0.846
β_P	27.9	0.01	0.081	Spatial distance	7.74e-06	0.278
				Time	1.41e-02	0.003
				Elevation	3.62e-05	0.827
				Slope	3.19e-03	0.561
				Aspect	2.31e-03	0.798
β_H	86.9	0.04	<0.001	Spatial distance	-5.05e-07	0.402
				Time	-4.46e-03	0.001
				Elevation	-1.74e-05	0.261
				Slope	-2.28e-06	0.995
				Aspect	3.85e-04	0.714
β_0	99.5	0.05	<0.001	Spatial distance	-5.80e-08	0.900
				Time	-2.87e-03	0.001
				Elevation	-1.60e-05	0.116
				Slope	3.32e-04	0.252
				Aspect	-2.43e-04	0.700

Table A5. Interaction turnover partitions across abiotic gradients as tested by Multiple Matrix Regressions for all non-Syrphid Diptera. F stat and R^2 for each full model are below their respective β . The p-values that are <0.05 appear in boldface. $F_{5,10290}$ for all models.

Turnover partition	F	R^2	p	Variable	Estimate	p
β_{cc}	719.3	0.26	<0.001	Spatial distance	2.03e-06	0.108
				Time	2.92e-02	0.001
				Elevation	1.24e-04	0.001
				Slope	6.17e-04	0.457
				Aspect	3.02e-03	0.159
β_{PH}	115.5	0.05	<0.001	Spatial distance	-5.56e-06	0.396
				Time	3.27e-02	0.001
				Elevation	1.90e-04	0.265
				Slope	7.92e-04	0.873
				Aspect	2.00e-03	0.831
β_P	47.8	0.02	0.005	Spatial distance	7.24e-06	0.210
				Time	1.53e-02	0.001
				Elevation	1.19e-04	0.407
				Slope	-2.52e-03	0.566
				Aspect	6.24e-03	0.399
β_H	154.7	0.07	<0.001	Spatial distance	9.70e-07	0.328
				Time	-8.18e-03	0.001
				Elevation	-1.12e-04	0.001
				Slope	1.07e-03	0.096
				Aspect	-1.73e-03	0.261
β_0	278.9	0.12	<0.001	Spatial distance	-6.16e-07	0.526
				Time	-1.06e-02	0.001
				Elevation	-7.29e-05	0.002
				Slope	1.27e-03	0.064
				Aspect	-3.50e-03	0.031

Table A6. Interaction turnover partitions across abiotic gradients as tested by Multiple Matrix Regressions for Lepidoptera. F stat and R^2 for each full model are below their respective β . The p-values that are <0.05 appear in boldface. $F_{5,10290}$ for all models.

Turnover partition	F	R^2	p	Variable	Estimate	p
β_{cc}	647.0	0.24	<0.001	Spatial distance	2.28e-06	0.130
				Time	3.34e-02	0.001
				Elevation	1.42e-04	0.001
				Slope	4.54e-04	0.605
				Aspect	5.40e-03	0.049
β_{PH}	60.6	0.03	0.008	Spatial distance	-6.60e-06	0.398
				Time	2.57e-02	0.001
				Elevation	1.87e-04	0.351
				Slope	-3.71e-03	0.520
				Aspect	3.99e-03	0.690
β_P	27.0	0.01	0.093	Spatial distance	8.55e-06	0.223
				Time	1.41e-02	0.004
				Elevation	-1.53e-05	0.929
				Slope	3.70e-03	0.503
				Aspect	2.21e-03	0.815
β_H	92.9	0.04	<0.001	Spatial distance	3.87e-07	0.474
				Time	-3.97e-03	0.001
				Elevation	-2.25e-05	0.098
				Slope	2.71e-04	0.433
				Aspect	-3.45e-04	0.686
β_0	74.7	0.04	<0.001	Spatial distance	-4.62e-08	0.892
				Time	-2.53e-03	0.001
				Elevation	-7.55e-06	0.508
				Slope	1.92e-04	0.511
				Aspect	-4.54e-04	0.506

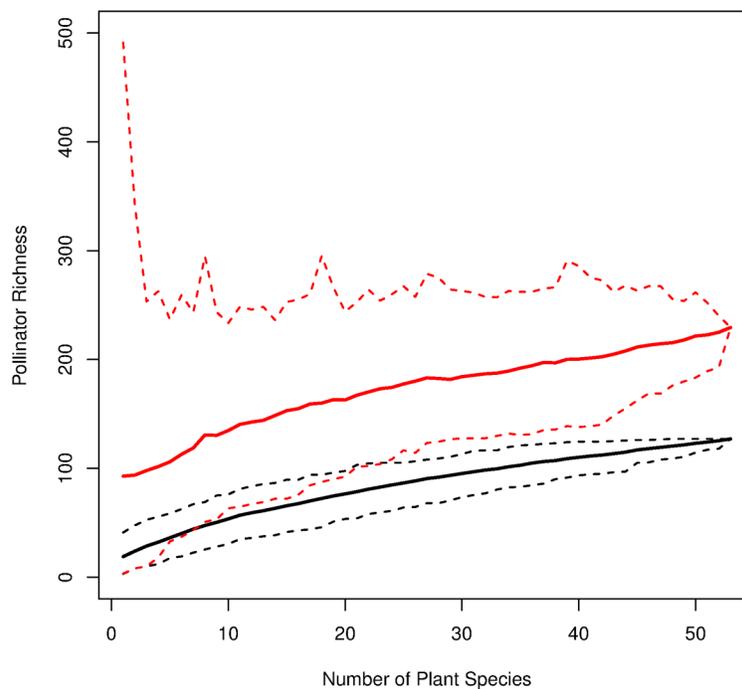


Fig. A1. Sampling completeness curve for plant-pollinator interactions, showing accumulated pollinator richness with increasing number of floral species. The black line represents the observed pollinator richness, while the red line represents estimated pollinator richness via the Chao estimator method. Dashed lines are 95% confidence intervals.

SUPPLEMENT

R scripts and species lists for plants and pollinators (*Ecological Archives* <http://dx.doi.org/10.1890/ES14-00323.1.sm>).