

"With a little help from my friends"

Phylogenetic distance as a predictor of floral visitation in the plant communities of Gothic, CO.

Student: Carlisle Evans Peck

Mentor: Ken Whitney

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Introduction

In recent years, a new conceptual framework in community ecology has emerged, focusing on phylogenetics as a major determining factor in community composition. The phylogenetic composition of a community can be very important in predicting interspecific interactions and community structure, even more so than species richness, the traditional metric of biodiversity (Jactel and Brockerhoff 2007). The new field of community and ecosystem genetics takes a "genes to ecosystems" approach to ecology which places ecosystems in an evolutionary framework and emphasizes how genetics structure interspecific interactions (Wymore et al 2011). Such an approach makes the evolutionary history of an ecosystem key to understanding its present state. Phylogeny may therefore be very important to the emergence of interspecific interactions.

There are several ways that closely related species may share floral visitors. Interactions with herbivores, pollinators, and nectar robbers are all based on the sensory capabilities of the animal, as influenced by the morphology of the plant. Pollination is perhaps the most familiar of the specialized plant/animal interactions. Flowering plants and their animal pollinators are known to have evolved together, though the level of specialization resulting from this

coevolution is still debated (Waser et al 1996). While this is a valid speculation, it is impossible to deny that the activity of pollinators is the most important agent of natural selection in plants (Johnson, Linder, and Steiner 1998; Stebbins 1970). Since pollination and other forms of plant-animal interactions are based on the sensory capabilities of the animal visitors, it follows that morphologically similar plants will attract similar visitors. This conclusion is found to be supported by past research when specialization is gauged by grouping pollinators into functional groups (ie: long tongued bees, short tongued bees, hummingbirds, etc.) instead of recording individual species. It becomes clear that many animal pollinated angiosperms have a very specialized relationship with a single functional group, if not a single species, supporting the concept of pollination syndromes (Fenster et al. 2004). In the metanalysis of pollination studies by Fenster et al. (2004), it was found that, of 278 entomophilous species, 150 were pollinated by a single functional group (Fenster et al. 2004). Even generalist pollinators may develop preferences for certain flowers, and studies of pollinator behavior suggest that they tend to avoid unfamiliar blooms, though it is possible for these habits to be broken (Forrest and Thomson 2009). It follows from the pollination syndrome concept that morphologically similar plant species will attract similar groups of pollinators, and this also applies to other plant/animal interactions such as herbivory (Ness et al. 2011). While morphological similarity is not necessarily a proxy for phylogenetic similarity and a single lineage of angiosperms may be characterized by differing pollination syndromes (Johnson, Linder, and Steiner 1998), a species' phylogenetic history does place some constraints on its evolutionary trajectory (Stebbins 1970) and may therefore be important in determining the number and identity of floral visitors. A study of 36 plant-pollinator and 23 plant-frugivore networks conducted by Rezende et al (2007) found that the number and identity of interactions were predicted by phylogenetic similarity in 24.8%

and 25% of plant phylogenies (Rezende et al 2007). This suggests that related plants will attract similar populations of pollinators and frugivores in similar abundances. If this is valid, there may in turn be a relationship between a species' phylogenetic distance to the others in its community and its success in pollination.

There are two explicitly contradictory ways in which the presence of a close relative may affect the performance of a species. Such phylogenetic proximity may both be beneficial to the success of a target species due to adequate adaptation to abiotic and biotic conditions already present in the community (ie: environmental filtering) and enhancement of mutualisms and interspecific interactions, as well as inhibit it through niche overlap and competition for resources (Thuiller et al 2010). The study conducted by Ness, et al (2011) demonstrated how close relatives in a community may occupy similar enough niches to experience similar effects (Ness et al 2011). They focused on how phylogeny affects herbivory on invasive and native species and found a positive correlation between the relatedness of a species to the native population and herbivory; that is, phylogenetically isolated species experienced relatively low rates of attack. Yet, the predicted effect of phylogenetic isolation on other ecological interactions, eg. pollinator visitation, is unclear. Contemporary research on pollination illustrates two possibilities. Closely related co-flowering species may encounter strong competition for pollinators as well as problems such as the clogging of pollen tubes due to the deposition of excessive amounts of heterospecific pollen (Schuett and Vamosi 2009). This suggests that phylogenetically isolated species may experience relatively low visitation rates. On the other hand, a close relative may benefit the pollination success of a focal species by attracting more pollinators to the community than would otherwise be there (Sargent et al. 2011). There is little consensus in the literature as to which of these two possibilities dominates pollination

communities. However, understanding the influence of phylogenetic diversity in a community on pollination is vital to understanding how these systems will respond to changes in community structure as a result of climate change and invasive species as any disruptions of phylogenetic structure could have wide reaching effects such as coextinctions of related species that depend on similar visitors (Rezende et al 2007).

Schuett and Vamosi (2009) and Sargent et al (2011) both conducted research on a single focal species in different communities containing different species with various levels of relatedness. We found that a community wide study was necessary to garner many points of data for phylogenetic distance in order to more directly compare this to floral visitation. This type of survey was suggested by Waser, et al (1996) to eliminate any false signal that may arise from isolating a single focal species for study (Waser et al 1996). Our study investigated whether or not there is a phylogenetic structure to the interactions between plants and their floral visitors. Here we ask: does phylogenetic isolation predict floral visitation rates in plant species? We conducted a widespread survey of the resident flora, including twenty-seven plant species from nineteen different families. The effort involved in such an extensive community-wide study necessitated a tradeoff: because it would be possible to determine the actual role of each visitor (pollinator, nectar robber, florivore, etc.) for only a small number of plant species, we focus on general floral visitation rates without quantifying roles for a large number of species. This metric is related to, but not the same as, pollination success, as it includes non-pollinators and incidental pollinators (ie: florivores or resting insects) as well as actual pollinators. The large selection of species allowed comparison of visitation rates for a wide range of species in a single habitat and therefore many data points for phylogenetic distance and visitation rate were obtained in order to more directly compare the two variables. It was predicted that species with either very high or

very low phylogenetic distances to the rest of the plant community will experience low visitation rates due to competition for visitors and isolation, respectively, and that the highest floral visitation rates will be found in species with intermediate phylogenetic distances to the species in the larger community, as they will avoid the hindrances of competition and isolation found at either extreme.

Methods:

Floral visitation rates

All floral visitation data were collected in the area surrounding Gothic, Colorado, in and around the site of Rocky Mountain Biological Laboratory. The East River Valley where Gothic is situated is dominated by three subalpine plant communities: open meadows, Aspen (*Populus tremuloides*) forest, and coniferous forest (dominated by *Picea engelmannii* and *Abies bifolia*). My observation sites were restricted to the subalpine to montane habitats of the valley including the Gothic Townsite, Virginia Basin, the Maroon Bells Wilderness, Emerald Lake, and Washington Gulch Trail. The summer of 2012 was preceded by abnormally low snowpack and featured very little precipitation throughout the season, making for a very dry year with sparse vegetation and highly advanced phenology. This put special constraints on the abundance and flowering time of plant species.

Data were collected on 27 species in two distinct time periods, the first between 6/18/12 and 7/13/12 and the second between 7/16/12 and 8/3/12 (Table 1). The identities of these species were verified with the help of *Wild About Wildflowers* (Darrow 2006) and *Colorado Flora: Western Slope* (Weber and Whitman 1996). Family names were updated to the APG III angiosperm taxonomy (APG 2009). The species lists in each time period were intended to be

wholly distinct. Target species were selected based on their abundance (and therefore on their ability to provide a sufficient amount of data) but were limited to two species per family in order to create phylogenetic spread in the dataset. These were selected from *Vascular Plants of the Gothic Area* (Frase and Buck 2007). A voucher specimen of each species was collected and processed.

Observations were split into 6 different forty minute observation periods per species. Three separate populations of each species in distinct sites were selected for observation, and one to four individuals (or, in the case of large shrubby plants, portions of plants) were observed simultaneously at each site for approximately forty minutes on each of two days. The minimum distance between sites was approximately a ten to fifteen minute walk, and most of the sites were much farther apart than this. All observation was conducted between 10 AM and 5 PM on either sunny or partly cloudy days, the times when potential floral visitors are active. Each site was observed for this duration at three separate times: one time each between 10 AM and 12 PM, 1 PM and 3 PM, and 3 PM and 5 PM. Number of floral visitors was recorded, and they were identified and placed into the following categories: dipterans, hymenopterans, and lepidopterans, and "other insects". No bird visitation was observed during this study. The number of flowers or inflorescences observed, the number of flowers per inflorescence, and the total number of flowers or inflorescences on each plant were recorded. Floral characteristics such as height of the tallest inflorescence off the ground and floral volume (LxWxH) were also measured. The local conspecific density of flowers or inflorescences of the focal species at each site was measured by counting the number of flowers or inflorescences in a 25 m², 4 m², and, in one instance, 1 m² area around the focal individuals. The smaller plots were utilized for extremely abundant plants

with small inflorescences such as *Galium boreale* or *Hackelia floribunda*. The other species flowering in the visible area of the plot were also noted.

Because comparisons of visitation rates are complicated by morphological differences between plant species, three different visitation rates were analyzed, with visitation rates being calculated by averaging across all of the above observations of a given focal species: 1) rates to individuals (no. visitors/plant/min), rates to inflorescences (no. visitors/inflorescence/min), and rates to individual flowers (no. visitors/flower/min).

Estimation of phylogenetic distances

A list of all the animal pollinated plant species in the Gothic Area was created from Fraser and Buck (2007). From the complete angiosperm list, all non-animal pollinated taxa were excluded, such as those in the families Betulaceae, Cyperaceae, Juncaceae, Poaceae, Typhaceae, Juncaginaceae, Salicaceae, and the genus *Potamogeton*. A phylogenetic tree for this species list was then created using the Phylomatic web service (Webb and Donoghue 2005) and imported into Mesquite ver. 2.75 (Maddison and Maddison 2009). Fossil-based branch lengths (in millions of years) were obtained from Wikstrom et al. (2001). Phylocom (Webb et al. 2008) was used to generate a phylogenetic distance matrix for all species, from which we calculated the average phylogenetic distance between each of our focal species and all of the remaining animal pollinated species in the region, as well as the phylogenetic distance to each focal species' closest relatives. Two phylogenetic metrics were then calculated: the distance to the nearest phylogenetic neighbor (nearest neighbor distance, NND) and the mean phylogenetic distance (MPD) to all species in the community. We also investigated two alternative measures of phylogenetic distance (mean inverse phylogenetic distance and inverse nearest neighbor

distance, see Ness et al. 2011), but as these metrics performed similarly to MPD and NND, they were not used in the final analyses.

Examination of the relationship between phylogenetic isolation and floral visitation

Because an initial regression found no significant relationship between visitation rate and date, we opted to include all species in the same analysis rather than splitting species by observation period (late June and early July vs. late July) and doing two sets of analyses. We also made the decision to lump all visitors together for this set of analyses; future analyses will examine patterns for individual groups (bees, flies, etc.). For each plant species across all observation dates, visits were totaled and observation effort (minutes) was calculated. Visitation rates to each species were then quantified as visitation per individual (plant) minute (PINM), visitation per inflorescence minute (PIFM), and visitation per flower minute (PFM). A multiple regression analysis was then run on each of these three visitation rates, with two measures of phylogenetic distance (NND, MPD), local density, floral volume, and inflorescence height as predictor variables. A model selection process was then conducted and AIC values were used to determine which combination of the five predictor variables remained in each final model. Partial regression plots were then generated for our main predictors of interest (MPD, NND); these plots isolate the effect of the variable in question by accounting for the confounding effects of the other variables in the model (Rawlings et al. 1988).

Results

Visitation per Individual Minute

The best fit model for visitation per individual (plant) minute included inflorescence height as the sole predictor variable and explained 34.64% of the variation in visitation ($p=0.0010$, $R^2=0.3464$) (Table 2). The relationship between inflorescence height and visitation PINM was found to be positive (standardized slope=0.101) (Fig. 2).

Visitation per Inflorescence Minute

The best fit model for visitation per inflorescence minute (visitation PIFM) included mean phylogenetic distance (MPD), nearest neighbor distance (NND), conspecific density, and inflorescence density as predictor variables and explained 35.23% of the variation in visitation ($p=0.0342$, $R^2=0.3523$) (Table 3). A negative relationship was found between MPD and visitation PIFM (standardized slope=-0.023) (Fig. 3). A positive trend was found between NND and PIFM (standardized slope=0.020) (Fig. 3). Conspecific density and inflorescence volume also had influences on visitation PIFM (standardized slope=-0.020; standardized slope=0.018)

Visitation per Flower Minute

The best fit model for visitation per flower minute (visitation PFM) included MPD, NND, and conspecific density as predictor variables and explained 26.72% of the variation in visitation ($p=0.0548$, $R^2=0.2672$) (Table 4). A positive relationship was found between NND and visitation PFM (standardized slope=0.025) (Fig. 4). A negative trend was found between MPD and visitation PFM (standardized slope=-0.019) (Fig. 4). A negative trend was also found between conspecific density and visitation PFM (standardized slope=-0.020).

Discussion

The goal of this study was to determine if the phylogenetic isolation of a plant species is correlated with its floral visitation rates. Previous studies have shown that pollination success for a single focal species is influenced by the phylogenetic diversity of a plant community (Schuett and Vamosi 2009; Sargent et al 2011), yet to our knowledge no community-wide research on floral visitation and phylogenetic distance has been conducted. We predicted that intermediate phylogenetic distances would exhibit the highest visitation rates. While this result was not found, our results nonetheless show that floral visitation rates are correlated with phylogenetic distance. We found that MPD and NND have opposite effects on visitation PIFM and PFM. Visitation PIFM and PFM increased with decreasing MPD, while they increased with increasing NND (Figs. 3, 4). While seemingly contradictory, these results are actually entirely compatible. They suggest that, while the presence of many relatives increases visitation in a plant species (perhaps by attracting additional pollinators), the presence of a very close relative is detrimental to visitation (perhaps through competition for pollinators). Therefore, it appears that facilitation and competition are occurring simultaneously. Our results could resolve the contradiction found in the studies of Schuett and Vamosi (2009) and Sargent, et al. (2011) which, respectively, suggest that the presence of close phylogenetic relatives has a competitive and facilitative influence on pollination success (Schuett and Vamosi 2009, Sargent et al. 2011). This is the first study to find such a connection.

In both visitation PIFM and PFM, conspecific density was found to have a negative effect (Fig. 3, 4). This could be due to increased competition for visitors as a result of a high density of conspecifics in the area. Visitation PIFM was also positively influenced by inflorescence volume (Fig. 3) which could indicate that larger and more conspicuous flowers attract more visitors.

It is curious that no correlation with phylogenetic distance was found in visitation per individual minute (PINM). As of now, we are unsure of why this result is inconsistent with the others. It is not surprising, however, that inflorescence height had a significant positive effect on visitation, it has been demonstrated in previous studies that taller plants have greater reproductive success (Carromero and Hamrick 2005).

Some of the relationships found between phylogenetic distance and floral visitation are weak (ie., marginal significance levels of $0.10 > p > 0.05$). Recall that the summer of 2012 was an abnormal one, and any interpretation of these results must take this into account. A dearth of snowpack, early snowmelt, advanced phenology, and drought all had drastic effects on the ecosystem found at Gothic. Hegland et al (2008) suggest that advanced phenology, such as that found in 2012, may completely disrupt plant-pollinator interactions since the emergence of both often depends on snowmelt and temperature. They found that insect phenology often advances more than plant phenology in abnormal years. Furthermore, they claim that "such a phenological decoupling may result in the emergence of novel plant-pollinator interactions" (Hegland et al 2008). Such a collapse of traditional plant-pollinator relationships may have occurred in the Gothic area this year, resulting in relatively weak patterns for phylogenetic distance.

However, further research should be conducted in this field. It may be useful to conduct replicated studies over multiple growing seasons to see if the effects of phylogenetic distance on floral visitation rates are weaker or stronger in more "normal" years vs. dry years. The effect of density of coflowering species on visitation should also be investigated. Inclusion of this variable may result in a clearer signal of phylogenetic isolation. Also, other measurements of pollination success should be investigated such as pollen deposition or seed set as these may elicit different results than floral visitation rate. Thomson (1982) demonstrates that visitation increases with

increasing density of conspecifics, while seed set peaks at intermediate densities, suggesting that these two variables are not synonymous, and should both be studied (Thomson 1982). Another question that we seek to answer in the future is whether or not floral visitation rates exhibit a phylogenetic signal, meaning that closely related species have similar visitation rates. This is possible using the existing dataset, so no new data are needed.

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References

- Angiosperm Phylogeny Group. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* 161:105-121.
- Carromero W and Hamrick JL. 2005. The mating system of *Verbascum thapsus* (Scrophulariaceae): the effect of plant height. *International Journal of Plant Sciences*. 166(6):979-83.
- Darrow C. 2006. *Wild about wildflowers*. 2nd edition. Glendale, AZ: WildKat Publishing Co.
- Fenster CB et al. 2004. Pollination syndromes and floral specialization. *Annu. Rev. Ecol. Evol. Syst.* 35:375-403.
- Forrest J and Thomson JD. 2009. Pollinator experience, neophobia and the evolution of flowering time. *Proc R Soc B* 276:935-43.
- Fraser BA, Buck P. 2007. *Vascular plants of the Gothic area*. Gothic, CO: Rocky Mountain Biological Laboratory; p 4-28.
- Hegland, et al. 2009. How does climate warming affect plant-pollinator interactions. *Ecol Lett* 12:184-195.
- Jactel H and Brockerhoff EG. 2007. Tree diversity reduces herbivory by forest insects. *Ecol Lett* 10:835-848.
- Johnson SD, Linder HP and Steiner KE. 1998. Phylogeny and radiation of pollination systems in *Disa* (Orchidaceae). *American Journal of Botany* 85(3): 402-11.

Maddison WP and Maddison DR. 2009. Mesquite: a modular system for evolutionary analysis.

<<http://mesquiteproject.org>>

McCall C and Primack RB. 1992. Influence of flower characteristics, weather, time of day, and season on insect visitation rates in three plant communities. *American Journal of Botany* 79(4):434-42.

Ness JH, Rollinson EJ, and Whitney KD. 2011. Phylogenetic distance can predict susceptibility to attack by natural enemies. *Oikos* 120:1327-34.

Rawlings J, Pantula S, and Dickey D. 1988. *Applied Regression Analysis*. Wadsworth.

Sargent RD et al. 2011. Effect of local community phylogenetic structure on pollen limitation in an obligately insect pollinated plant. *American Journal of Botany* 98(2): 283-9.

Schuett EM and Vamosi JC. 2010. Phylogenetic community context influences pollen delivery to *Allium cernuum*. *Evol Biol* 37: 19-28.

Silberbauer-Gottsberger I, Gottsberger G, and Webber AC. 2003. Morphological and functional flower characteristics of New and Old World Annonaceae with respect to their mode of pollination. *Taxon* 52(4):701-18.

Stebbins GL. 1970. Adaptive radiation of reproductive characteristics in angiosperms, I: pollination mechanisms. In: *Annual Review of Ecology and Systematics* 1.

Thomson J. 1982. Patterns of visitation by animal pollinators. *Oikos* 39(2):241-50.

Thuiller W, et al. 2010. Resolving Darwin's naturalization conundrum: a quest for evidence. *Diversity Distrib* 16:461-75.

Waser NM, et al. 1996. Is pollination generalized? *Ecology* 77(4):1043-60.

Webb CO and Donoghue MJ. 2005. Phylomatic: tree assembly for applied phylogenetics. *Mol. Ecol. Notes* 5:181-3

Webb CO et al. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* 24:2098-100

Weber WA and Wittman RC. 1996. *Colorado flora: Western Slope*. 2nd ed. Niwot, CO: University Press of Colorado.

Whitney KD. 2009. Comparative evolution of flower and fruit morphology. *Proc R Soc B* 2:2941-7.

Wikstrom N et al. 2001. Evolution of the angiosperms: calibrating the family tree. *Proc R Soc B* 268: 2211-20.

Wymore AS, et al. 2011. Genes to ecosystems: exploring the frontiers of ecology with one of the smallest biological units. *New Phytologist* 191:19-36.

Tables and Figures

Time period	Species	Family	Mins. of observation
6/18/12 - 7/13/12	<i>Aquilegia coerulea</i>	Ranunculaceae (Darrow 2006, APG III 2009), Helleboraceae (Weber 1996)	280
	<i>Castilleja miniata</i>	Scrophulariaceae (Darrow 1996, Weber 2006) Orobanchaceae (APG III 2009)	240
	<i>Cymopterus lemmonii</i> (Darrow 2006) <i>Pseudocymopterus montanus</i> (Weber 1996)	Apiaceae	240
	<i>Erigeron elatior</i>	Asteraceae	240
	<i>Eriogonum umbellatum</i> var. <i>majus</i>	Polygonaceae	200
	<i>Erysimum capitatum</i>	Brassicaceae	160
	<i>Geranium richardsonii</i>	Geraniaceae	240
	<i>Helianthella quinquenervis</i>	Asteraceae	200
	<i>Ligusticum porteri</i>	Apiaceae	240
	<i>Linum lewisii</i>	Linaceae	241
	<i>Polemonium foliosissimum</i>	Polemoniaceae	160
	<i>Potentilla gracilis</i>	Rosaceae	240

	<i>Zigadenus elegans</i>	Liliaceae (Darrow 2006), Melanthiaceae (Weber 1996, APG III 2009)	198
7/16/12 - 8/3/12	<i>Arenaria congesta</i>	Caryophyllaceae	120
	<i>Campanula rotundifolia</i>	Campanulaceae	200
	<i>Chamerion angustifolium</i>	Onagraceae	200
	<i>Delphinium barbeyi</i>	Ranunculaceae (Darrow 2006, APG III 2009) Helleboraceae (Weber 1996)	200
	<i>Galium boreale</i> (Darrow 2006) <i>Galium septentrionale</i> (Weber 1996)	Rubiaceae	240
	<i>Gentiana parryi</i> (Darrow 2006) <i>Pneumonanthe parryi</i> (Weber 1996)	Gentianaceae	80
	<i>Gentianopsis thermalis</i>	Gentianaceae	200
	<i>Hackelia floribunda</i>	Boraginaceae	159
	<i>Linaria vulgaris</i>	Scrophulariaceae (Darrow 2006, Weber 1996) Plantaginaceae (APG III 2009)	80
	<i>Lupinus argenteus</i>	Fabaceae	200
	<i>Mertensia ciliata</i>	Boraginaceae	198
	<i>Pedicularis racemosa</i>	Scrophulariaceae (Darrow 2006, Weber 1996) Orobanchaceae (APG III 2009)	160

	<i>Saxifraga odontoloma</i> (Darrow 2006) <i>Saxifraga rivularis</i> (Weber 1996)	Saxifragaceae	200
	<i>Trifolium repens</i>	Fabaceae	40

Table 1: All of the species observed and their respective families. Where no reference is given, there was agreement between Darrow, Weber, and APG III on the family name. The total minutes of observation per species is also indicated.

	Standardized Parameter Estimate (slope)
Inflorescence Height	0.101

Table 2: The variable included in the best fit model for visitation per individual.

	Standardized parameter estimate (slope)
Mean phylogenetic distance	-0.023
Nearest neighbor distance	0.020
Conspecific density	-0.020
Inflorescence volume	0.018

Table 3: The variables included in the best fit model for visitation per inflorescence minute.

	Standardized parameter estimate (slope)
Mean phylogenetic distance	-0.019
Nearest neighbor distance	0.025
Conspecific density	-0.020

Table 4: The variables included in the best fit model for visitation per flower minute.

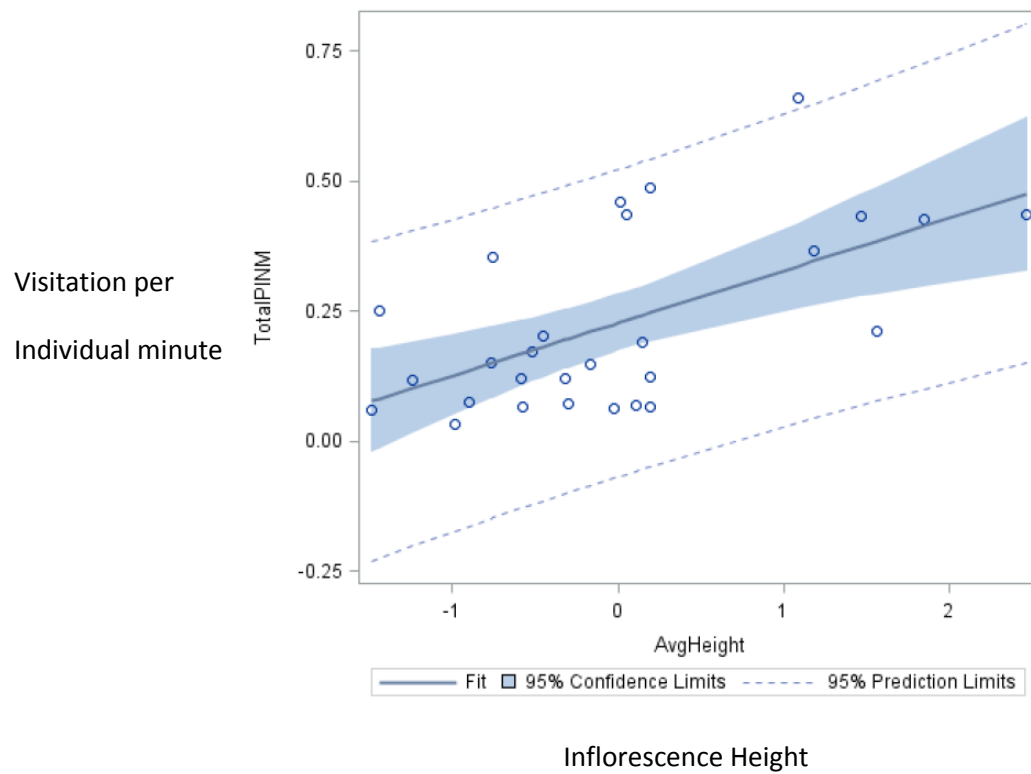


Fig. 2: The best fit model for visitation per individual included inflorescence height as a predictor variable ($p=0.0010$, $R^2=0.3464$). A positive relationship was found between the variables (slope=0.101). Points represent a species. Note: the x-axis has been standardized.

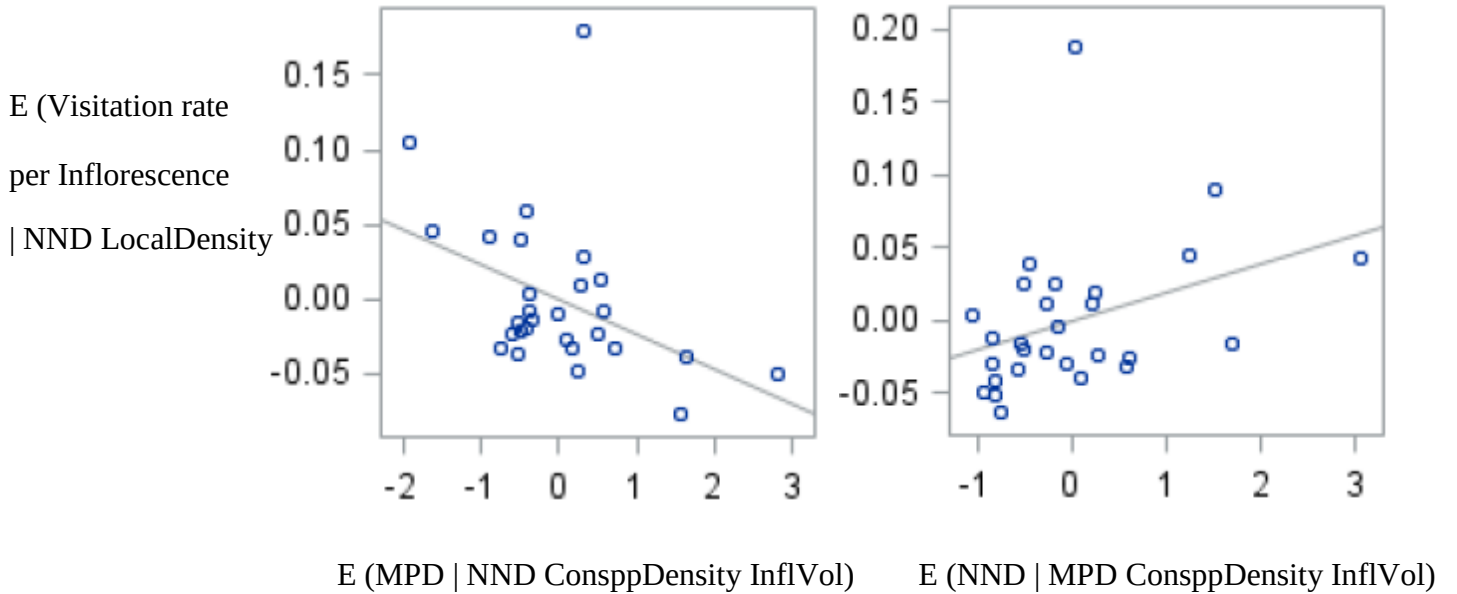


Fig. 3. The best fit model for visitation per inflorescence minute included MPD, NND, conspecific density, and inflorescence volume as predictor variables ($p=0.0342$ $R^2=0.3523$). Partial regression plots show that MPD has a negative relationship with visitation per inflorescence minute (slope=-0.023), while NND has a positive relationship with visitation per inflorescence minute (slope=0.020). The standardized x-axis represents the residuals of the independent variable (in this case, MPD or NND, listed to the left of the vertical bar) from a model that regresses it on the remaining independent variables (listed to the right of the vertical bar). The y-axis represents the residuals of the response variable calculated with the independent variable omitted.

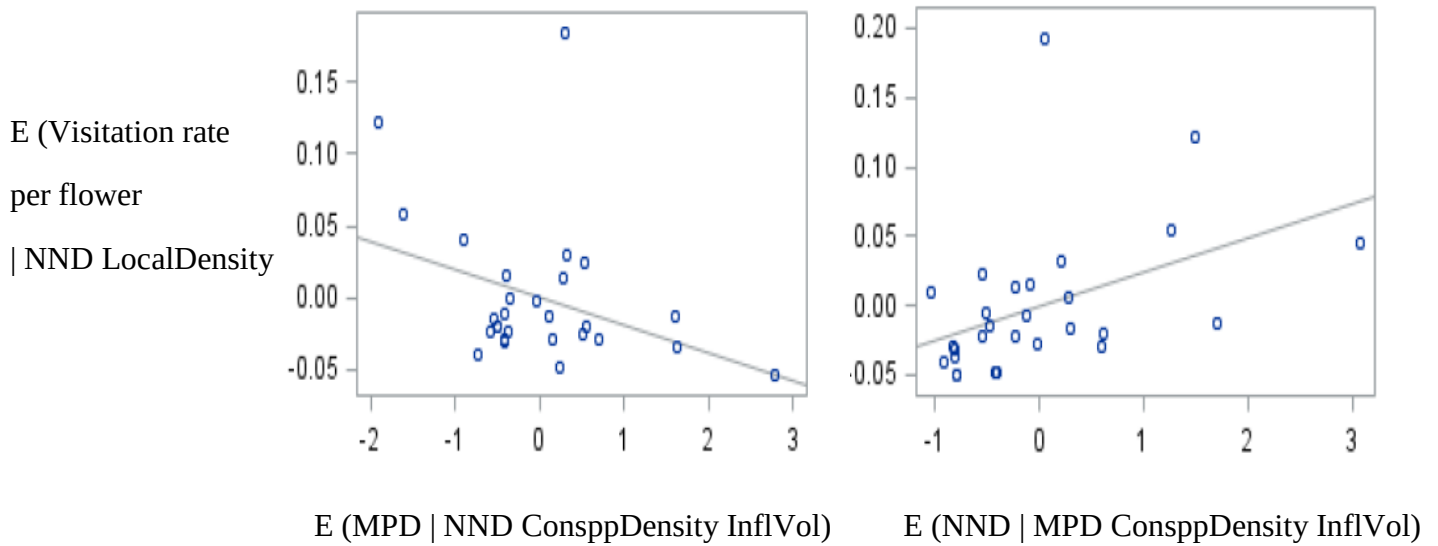


Fig. 4. The best fit model for visitation per flower minute included MPD, NND, conspecific density as predictor variables ($p=0.0548$, $R^2=0.2672$). Partial regression plots show that MPD has a negative relationship with visitation per inflorescence minute (slope=-0.019), while NND has a positive relationship with visitation per inflorescence minute (slope=0.025). Note: the x-axes are standardized.