Niche overlap decreases with increasing resource availability in a tropical plant-pollinator network.

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# Introduction

Many species feed on a subset of available resources and have distinct morphological and behavioral adaptations shaped by natural selection. By minimizing niche overlap, species reduce interspecific competition and can co-occur with potential competitors. Ecological specialization, such as species feeding on a narrow set of available resources, promotes community stability by setting differing limiting factors for each species (Levins). In addition, ecological specialization is a proposed explanation for latitude diversity patterns (), the evolution of higher taxa () and the diversity of life ().

Species resource breadth is determined by the availability of preferred resources, as well as the morphological adaptations that promote resource extraction. Niche theory suggests that potential competitors can coexist through niche differentiation. These differences will lead to disruptive selection in functional morphology and foraging behavior (MacArthur and Levins 1967, Abrams 1983). At times of low resource availability, species cannot be choosy and must forage on whatever resources are available. When resource availability is high, species should reduce interspecific competition by eliminating potential competitors through prioritizing exclusive resources.

In contrast, optimal foraging theory suggests that niche overlap should increase as available resources increases. When there are an abundance of available resources, species suffer reduced energy loss from exploitative competition (). Local patches are resource rich and difficult to exhaust. Assuming preferred resources are evenly spaced throughout the habitat, species should reduce time spent between patches as they minimize foraging for their specialized resource and choose more general resources.

While morphological adaptations for foraging are well known and pervasive in the nature world, the importance of functional tradeoffs remains understudied. It is widely assumed that species have adapted morphologies to fit their preferred resources, and that these adaptations come at cost of generalization. However, behavioral plasticity, as well as the presence of easy to use resources, may undermine these assumptions. For example, detailed study of the cranial morphology of cichlid fishes suggest highly specialized behavior, but field observations showed wide generalization and foraging breadth (Liem’s Paradox () ). Wilson (1998) suggested that this and similar examples () undermine the assumption of tradeoffs in foraging efficiency, and that the presence of abundant and easy to use resources come at no cost for morphological specialization. Since species can always fall back on these resources, they can afford to specialize to gain access to more difficult to use resources.

In this paper, we consider these opposing views and evaluate whether species niches widen or contract during periods of high resource availability using time-series data on Ecuadorian hummingbirds and their food plants from a tropical montane forest. In addition to measuring changes in niche overlap and network connectance, we evaluate the rate of morphological matching between hummingbird bill and corolla lengths.

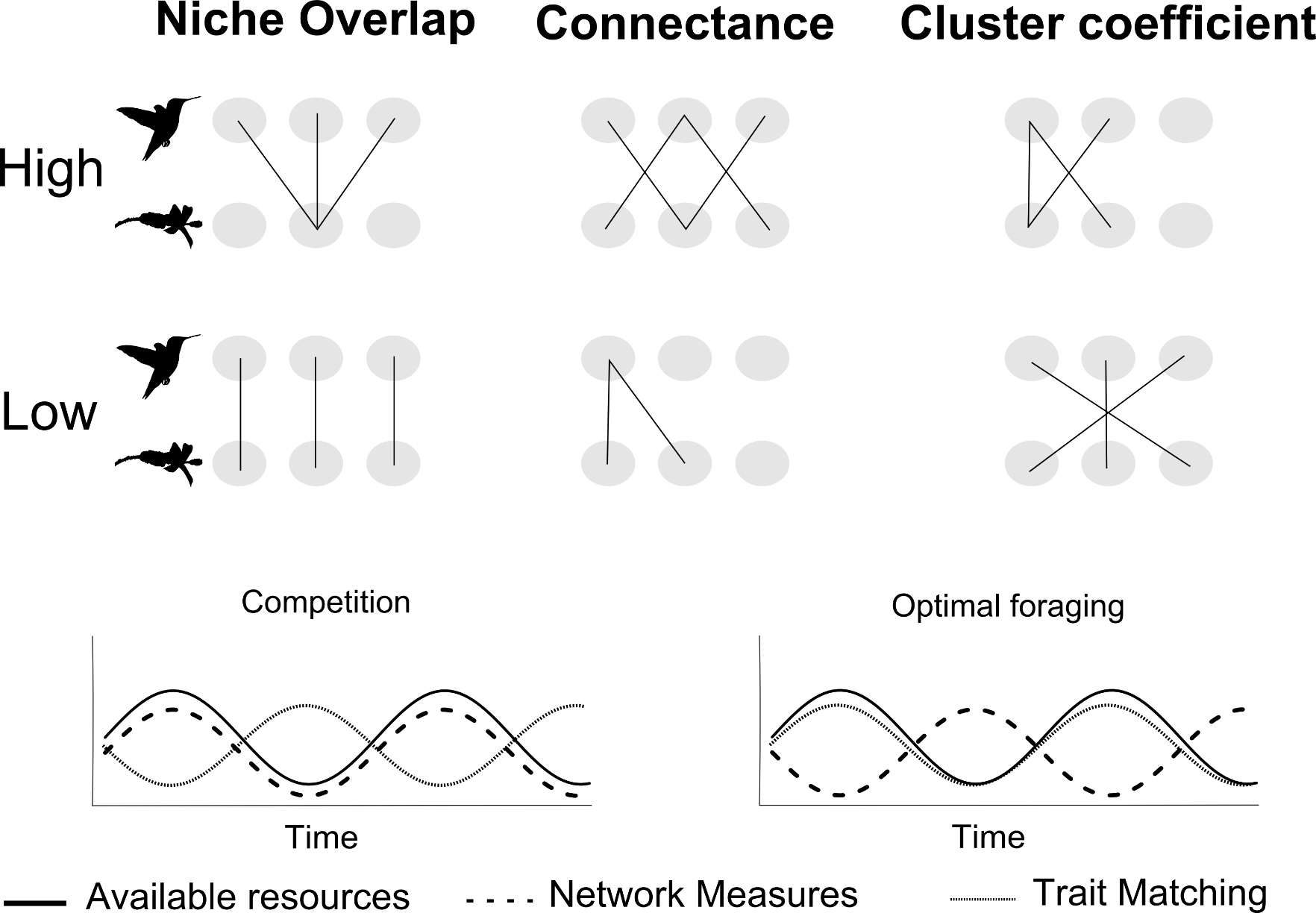
The dominant theory for pollinator niche breadth posits that selection should promote adaptations for the most effective pollinator (Stebbins 19XX). However, this hypothesis ignores how a pollinator interacts with the surrounding biotic environment and assumes that fitness costs based on morphological tradeoffs are constant throughout the year (Thomson 2003). In hummingbirds tradeoffs are manifested in morphological traits, where species tend to forage on corollas that match their bill length (Stiles et al. 1978; Vizentin-bugoni et al. 2014). Mismatches in bill morphology reduce foraging efficiency, creating an inverse relationship between specialized morphology and niche breadth (Maglianesi et al. 2014). We therefore expect that as niche breadth increases, the strength of phenotypic matching should decrease. When given a choice, we expect species should pick the flowers which reduce competition and closely match their bill morphology.

In tropical montane forests, flower availability changes drastically throughout the year (Stiles 1975), with spikes often occurring at the end of rainy season. In this study, we define our niche axis as the diversity of plants visited by a hummingbird species and specialization as the diversity of plants visited versus the number of available plant species. To test these hypothesis, we measured available resource using bi-monthly transects along a wide elevation gradient (1300-2500m). In addition, we harnessed novel time-lapse photography to monitor hummingbird visitation to flowers. We adopted a network modeling approach to measure niche overlap, network connectance and clustering as a function of available resources.

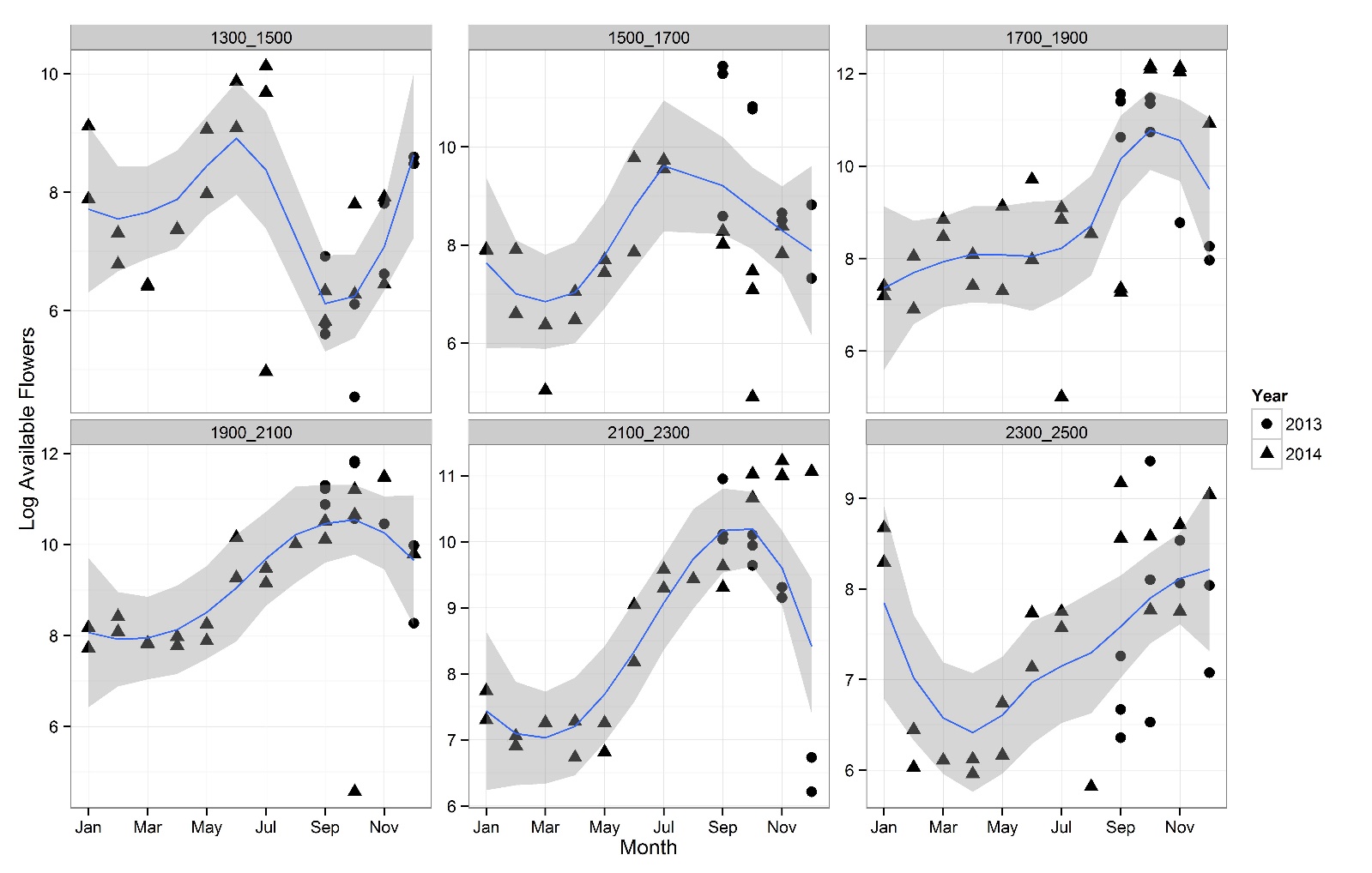
# Methods

* Study site
  + Data were collected at the Maquipucuna Research Station and Santa Lucia Ecolodges, Ecuador (0.118 S,-78.612 W) between June 2013 and July 2015 and August 2013 along an elevation gradient from 1300 m to 2500 m. The area contains regenerating secondary and primary cloud-forest, and has a warmer dry season from June to September (Webster and Rhodes 2005).
* Plant resources
  + To measure available resources, we counted the number of hummingbird pollinated plants within 5 m of pre-established trails along six 1 km transects. Each transect covered approximately 200 m of elevation change. For each plant, we estimated the number of total flowers by taking the average number of flowers on 3-5 stalks and multiplying this value by the total number of stalks on a plant. Surveys were repeated two times a month. All hummingbirds visiting flowers were noted during these transects and tagged with a GPS point.
* Hummingbird plant interactions
  + We used time-lapse cameras to monitor hummingbird visitation. Flowers in bloom were noted during each transect, and cameras were placed 1-3 meters from focal flowers. Cameras turned on automatically at dawn and recorded an image every second for at least two days.
  + We used the computer vision program MotionMeerkat to identify images where hummingbirds were observed (Weinstein 2014).
* Network Analysis
  + Measures of niche overlap
    - Niche Overlap
      * Distance metric to be used to calculate niche overlap. Any of **vegan**'svegdist-metrics can be used; defaults to Horn's index, which is the recommendation of Krebs (1989)
      * Mean similarity in interaction pattern between species of the same level, calculated by default as Horn's index (dist="horn").
    - Connectance
      * Realised proportion of possible links (Dunne et al. 2002): sum of links divided by number of cells in the matrix
    - Clustering
      * The cluster coefficient for a network is the average cluster coefficients of its members, i.e. simply the number of realised links devided by the number of possible links. Introduced by Watts & Strogatz (1998)
  + Why was each measure chosen?
* Null models
  + To address sampling constraints (Blüthgen 2010)
  + Randomization Methods

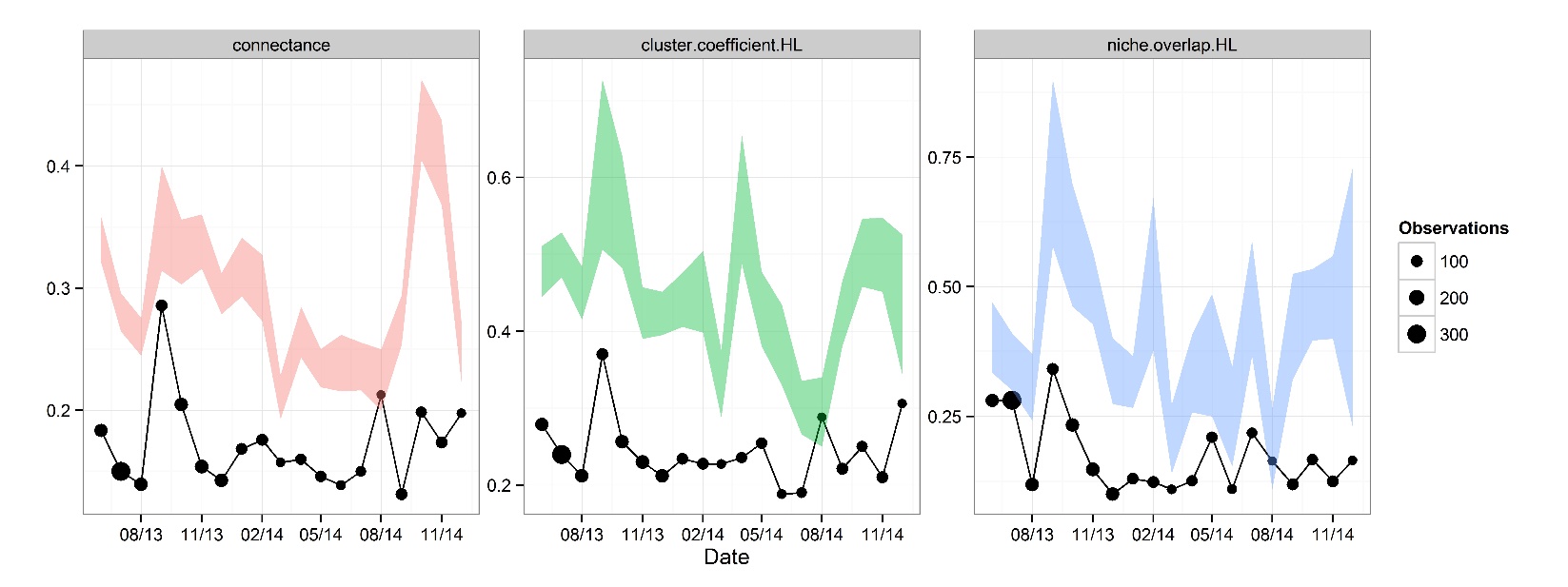
**Figure 1. Conceptual figure showing patterns of interactions between birds and flowers for high and low niche overlap, connectance and clustering. The bottom panel shows two hypothesized relationship between available resources, specialization, and trait matching.**

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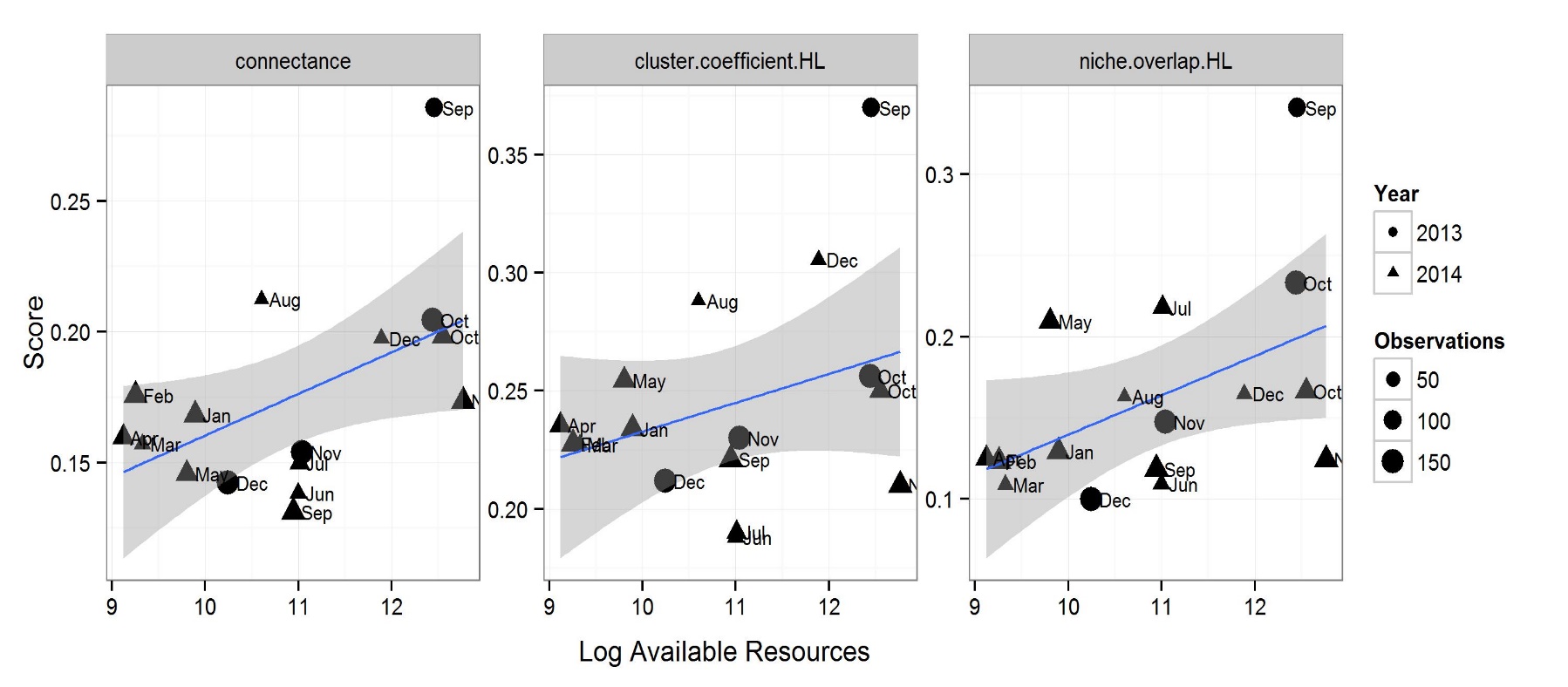
**Figure 2. Flower abundance per month for each transect.**



**Figure 3. Measures of hummingbird plant interactions through time (points) as compared to a null model maintaining the number of observations (shaded region).The size of the point is proportional to the number of interactions measured for each month.**

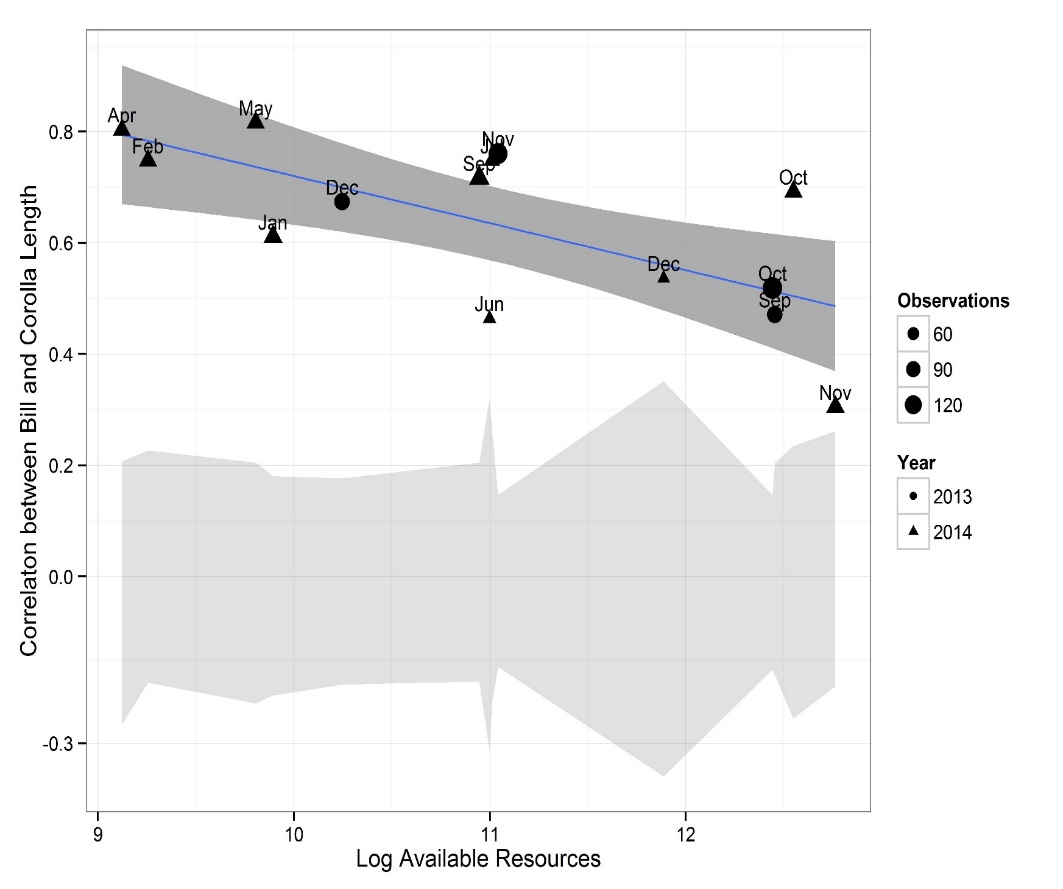


**Figure 4. Connectance, clustering and niche overlap as a function of available resources. Point size is proportional to number of interactions observed that month.**



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**Figure 4. The correlation coefficient among bill and corolla lengths decreases as a function of time (left) and available resources (right). The gray ribbon is a null randomization of the correlation structure which maintains the number of interactions per month.**



**Figure 6. Difference between bill length and corolla length for high and low abundance times. High abundance times are defined as months with 75th or higher quartile of flower abundance for each hummingbird species.**

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# Results

* How many plant records?
* How many bird records?
* How many interactions?
* Network Measures as a function of resources (and by species type?)
  + Niche Overlap
  + Connectance
  + Clustering
* Randomization Approach
* Trait Matching
  + Correlation
* Long and Short Billed Species

# Discussion

* Niche Overlap increases with available resources
* Trait Matching decreases with available resources
* Support for Wilson’s Solution liem’s paradox
* Coevolution and pollination web

Network ecology is a rapidly growing field used to infer ecological specialization. A variety of specialization metrics have been proposed (reviewed by Poisot et al 2014), yet it is unclear what the evolutionary implications are for most indices. For example, consider metrics which define specialization as choosing a narrow set of resources based on the abundance of resources selected by any player in the network (h2’ bluthgen, schluining). The logic is that species that choose a single, but highly abundant, resource are acting like gas particles, feeding on whatever resource they come into contact. While this is a logical definition of specialization, it has several biological obstacles.

To illustrate, consider the Giant Panda (*Ursus* ). Giant Pandas feeds almost exclusively on bamboo(). Compared to its living bear relatives, it is specialized along the resource niche axis. It has pronounced morphological adaptations for bamboo feeding, and its bamboo diet has shaped its life history strategy and foraging behavior (). It is geographically specialized and is largely restricted to bamboo forests. Yet, paradoxically, using H2’ or other resource weighted measures of specialization – a panda would be an absolute generalist, since bamboo is the highly abundant resource in panda habitat. Applying a strict quantitative definition of resource specialization would yield a highly confusing result. This same logic can be applied to our hummingbirds; White-whiskered Hermits feed predominantly on *glossoloma purpuruem* and *columnea cineraea*. There are many other plant species in the area, but both the hummingbird and the plant are common only at the lowest elevations of our fieldsite. Given the diversity of resources available, as well as the pronounced morphological extreme of both bill and corolla shapes, it would be reasonable to assert that these species are specialists, yet given that they occur in a restricted area, and are reasonable common, a null modeling approach accounting for abundance would say the reciproical specialization is minimal.

Abundance cannot be so easily disentangled from the interactions its supports. If one definition of a mutualism is an interaction which leads to positive growth rates among partners (), then abundance is the outcome of interaction, not a null model defining the interaction. This is easiest to conceptualize when thinking about an absolute specialist plant-pollinator relationship. If the population size of a plant’s sole pollinator declined, we would expect pollination services to decrease, and the plant may suffer pollen limitation and reduced fitness. As the population sizes of both players decrease, this interaction would become rarer compared to the environment, and abundance weighted metrics of specialization would increase despite no change in the fidelity or strength of the relationship.

The goal of the randomizations used in this paper is to determine whether we have sufficient sampling to differentiate our interactions from random, giving that we have a finite number of interactions. Uneven or incomplete sampling will bias network statistics and understate the nestedness of ecological networks (). The next stage in network ecology is to merge the quantitative measures of network properties with evolutionary ecology theory. Our study shows that temporal change in niche overlap is …

One potential solution is to avoid the category of specialization, and focus more on the importance of plant-pollinator interactions. Does utilizing a given flower come at a morphological tradeoff? Is the interaction stable through time? By focusing more on the effects of biotic selection, we may be able to overcome a narrow focus on defining specialization, and reorient our focus on to the outcomes of specialization.

## Comparable literature

* Correa, S., & Winemiller, K. (2014). Niche partitioning among frugivorous fishes in response to fluctuating resources in the Amazonian floodplain forest. Ecology, 95(1), 210–224.
* In general, dietary shifts in response to changes in the availability of preferred foods reduced interspecific niche overlap and may be a mechanism that facilitates coexistence in this species-rich fish assem- blage. During the period of greatest fruit production, diets of all six species were dominated, to varying degrees, by fruits and seeds, yielding broadly overlap- ping trophic niches among species.
* Trait packing, coexsitance and tropical specialization
* This niche partitioning mechanism is central to many explanations of the latitudinal gradient in species diversity, i.e that greater resources lead to finer subdivision of niche space, and promotes reproductive isolation.
* In this paper we have avoided abundance weighted measures of specialization (see Schluening and Bluthgen) due to the ongoing confusion in this literature. Specialization seems often defined as the fidelity of interactions with respect the abundance of the partners. Quantatitive approachs to network specialization (see H2') only consider
* Dalsgaard, B., Magård, E., Fjeldså, J., Martín González, A. M., Rahbek, C., Olesen, J. M., … Svenning, J.-C. (2011). Specialization in plant-hummingbird networks is associated with species richness, contemporary precipitation and quaternary climate-change velocity. PloS One, 6(10), e25891. <doi:10.1371/journal.pone.0025891>
  + Historical effect on specialization.

# Literature Cited

Blüthgen, N. 2010. Why network analysis is often disconnected from community ecology: A critique and an ecologist’s guide. Basic and Applied Ecology 11:185–195.

Feinsinger, P., and R. Colwell. 1978. Community organization among neotropical nectar-feeding birds. American Zoologist 18:779–795.

Lever, J. J., E. H. van Nes, M. Scheffer, and J. Bascompte. 2014. The sudden collapse of pollinator communities. Ecology letters 17:350–9.

Maglianesi, M., N. Blüthgen, K. Böhning-Gaese, and M. Schleuning. 2014. Morphological traits determine specialization and resource use in plant-hummingbird networks in the Neotropics. Ecology In press.

Petanidou, T., A. S. Kallimanis, J. Tzanopoulos, S. P. Sgardelis, and J. D. Pantis. 2008. Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. Ecology letters 11:564–75.

Schleuning, M., J. Fründ, and D. García. 2014. Predicting ecosystem functions from biodiversity and mutualistic networks: an extension of trait-based concepts to plant-animal interactions. Ecography n/a–n/a.

Stiles, F. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican Heliconia species. Ecology 56:285–301.

Stiles, F. G., S. Biotropica, N. Sep, D. C. Rica, C. Universitaria, C. Rica, F. La, et al. 1978. Temporal Organization of Flowering Among the Hummingbird Foodplants of a Tropical Wet Temporal Organization of Flowering among the Hummingbird Foodplants of a Tropical Wet Forest 10:194–210.

Thomson, J. 2003. When is it mutualism? The American Naturalist 162:S1–S9.

Vázquez, D. P., N. Blüthgen, L. Cagnolo, and N. P. Chacoff. 2009. Uniting pattern and process in plant-animal mutualistic networks: a review. Annals of botany 103:1445–57.

Vizentin-bugoni, J., P. K. Maruyama, and M. Sazima. 2014. Processes entangling interactions in communities: forbidden links are more important than abundance in a hummingbird–plant network. Proceedings of the Royal Society B: Biological Sciences 281.

Weinstein, B. G. 2014. MotionMeerkat: integrating motion video detection and ecological monitoring. (S. Dray, ed.)Methods in Ecology and Evolution n/a–n/a.

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