Persistent bill and corolla matching despite shifting temporal resources in tropical hummingbird-plant interactions

Abstract
By specialising on specific resources, species evolve advantageous morphologies to increase the efficiency of nutrient acquisition. However, many specialists face variation in resource availability and composition. Whether specialists respond to these changes depends on the composition of the resource pulses, the cost of foraging on poorly matched resources, and the strength of interspecific competition. We studied hummingbird bill and plant corolla matching during seasonal variation in flower availability and morphology. Using a hierarchical Bayesian model, we accounted for the detectability and spatial overlap of hummingbird-plant interactions. We found that despite seasonal pulses of flowers with short-corollas, hummingbirds consistently foraged on well-matched flowers, leading to low niche overlap. This behaviour suggests that the costs of searching for rare and more specialised resources are lower than the benefit of switching to super-abundant resources. Our results highlight the trade-off between foraging efficiency and interspecific competition, and underline niche partitioning in maintaining tropical diversity.

Keywords
Co-evolution, Ecuador, hummingbirds, networks, species interactions.

INTRODUCTION
Diet specialisation, the use of a subset of available resources, is considered one of the major mechanisms permitting species co-occurrence through reduced niche overlap (Gause 1934; MacArthur 1958; Chesson 2000; Levine & HilleRisLambers 2009). Diet specialists often have morphological adaptations that allow them to extract resources more efficiently as compared to species with generalist feeding morphologies (Futuyma & Moreno 1988; Forister et al. 2012). In mutualistic interactions, reciprocal morphological adaptations, such as between plant corollas and pollinator mouthparts, may result in trait-matching, in which species that have similar traits tend to interact more often (Thomson 2003; Stang et al. 2009; Vázquez et al. 2009; Bartomeus et al. 2016). From the perspective of a pollinator, using a plant with a well-matched trait increases its ability to efficiently extract nutrients (Feinsinger & Colwell 1978; Maglianesi et al. 2014; Sazatornil et al. 2016). Trait-matching is an important mechanism in shaping ecological communities across many mutualist systems (Stang et al. 2009; Dehling et al. 2014; Vizentin-Bugoni et al. 2014; González-Castro et al. 2015; Olito & Fox 2015), and may play a role in reciprocal co-evolution among plants and pollinators (Thomson 2003; Castellanos et al. 2004; Muchhala & Thomson 2009).

While the importance of trait-matching has been well documented, temporal variation in trait-matching is understudied. Species that rely on ephemeral resources, such as fruits and flowers, may have to cope with changes in the morphology of available resources (Jordano 1987; Yang et al. 2008; Correa & Winemiller 2014; Miller-Struttman & Galen 2014). It may therefore be challenging for species with fixed morphological adaptations to switch to more abundant resources that are poorly matched to their feeding morphology (Schoener 1971; Carnicer et al. 2008). By studying how seasonal changes in corolla morphology influence trait-matching, we can gain insight into the trade-off between the reduced foraging efficiency of feeding on poorly matched resources vs. the cost of searching for well-matched resources (Robinson & Wilson 1998; Sargent & Ackerly 2008). Here, we investigate the matching between hummingbird bill lengths and flower corolla lengths during annual cycles of flower abundance in a tropical cloud forest. When the difference between a hummingbird bill length and flower corolla length is small, the flower is considered a well-matched resource; if the difference is large, it is considered a poorly matched resource.

The relationship between trait-matching and resource availability depends on the composition of resource pulses, the morphological characteristics of these resources, and the foraging strategies of competing consumer species (Robinson & Wilson 1998; Northfield et al. 2010; Tinker et al. 2012). Niche theory suggests that consumer species should preferentially forage on well-matched resources due to low handling times and a superior ability to extract nutrients (MacArthur 1958; Holt et al. 1994; Chesson 2000). If seasonal pulses are dominated by well-matched resources, a consumer species should abandon poorly matched resources, leading to reduced niche overlap among morphologically different species (Fig. 1a). Alternatively, if seasonal pulses are dominated by poorly matched resources, but the negative impact of reduced foraging efficiency is minimal, a consumer species might reduce its preference for rarer well-matched resources (Robinson & Wilson 1998). This pattern would lead to increased niche overlap among morphologically different consumer species (Fig. 1b).
Finally, if the costs of foraging on poorly matched resources are large, then a consumer species may forage on well-matched resources regardless of relative resource availability (Wilson & Yoshimura 1994). In this scenario, there would be no change in niche overlap among morphologically different species through time (Fig. 1c).

To evaluate seasonal variation in trait-matching, we collected data on hummingbird-plant interactions from northwest Ecuador. Tropical hummingbirds and their food plants are quintessential examples of diffuse co-evolution, with hummingbirds foraging on flower corollas that tend to match their bill length (Feinsinger 1976; Maglianesi et al. 2014; Maruyama et al. 2014; Vizentin-Bugoni et al. 2014). In tropical montane forests, the timing of mass flowering is related to annual cycles of precipitation (Van schaik et al. 1993). In general, mid-elevation forests have spikes in flower abundance at the end of rainy season, with only a very small number of species in continuous flower (Hilty 1997). This pattern of flowering forces hummingbirds to choose among differing flowering plant species throughout the year (Stiles 1975).

One challenge in estimating trait-matching is collecting sufficient observations to differentiate between interactions that do not occur, and interactions that were not detected (Chacoff et al. 2012). By using multiple time-lapse cameras, followed by computer vision software to review footage, we were able to greatly increase our sampling effort (Weinstein 2015). To separate the probability of interaction occurrence from the probability of interaction detection, we used a hierarchical Bayesian approach that accounts for the detectability of hummingbird species. Similar to the N-mixture models developed in wildlife ecology (Royle 2004), we assumed that there is a true, but unobserved, number of interactions, and treated each day of camera filming as an attempt to capture this daily interaction rate among birds and flowers. This approach has three main benefits: it differentiates the probability of an interaction from the probability of observing an interaction, it captures the uncertainty in estimating interactions among plant and hummingbird species, and it fits a mechanistic relationship for species interactions based on trait-matching and resource availability.

**METHODS**

**Data collection**

Data were collected along a single elevation gradient between the Maquipucuna Research Station and Santa Lucia Ecolodges, Ecuador (0.118 S, –78.612 W) between June 2013 and October 2015, and again from April 2016 to July 2016. At this site, there is a cooler rainy season (December–May) and a warmer dry season (June–October). The site contains primary and regenerating cloud-forest and spans an elevation gradient from 1300 m to 2500 m. We divided this elevation gradient (Schoener 1971; Abrams 1991). Finally, if the costs of foraging on poorly matched resources are large, then a consumer species may forage on well-matched resources regardless of relative resource availability (Wilson & Yoshimura 1994). In this scenario, there would be no change in niche overlap among morphologically different species through time (Fig. 1c).

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into six 1 km transects that each spanned c. 200 m in elevation.

We conducted bi-monthly flower surveys along these transects to count hummingbird-visited flowers in bloom within 5 m of pre-established trails. Hummingbirds forage on a wide range of flowers, therefore it is difficult to use flower morphology and color (i.e., tubular corolla shape, red and purple color) to determine which flowers will be visited. We carefully evaluated all available flowers based on observations during the floral transects, camera recording sessions (see below), incidental records, field guides, and local expert knowledge. For each flowering plant, we either directly counted flowers or extrapolated flower abundance by multiplying the number of flowers on at least three stalks by the number of total stalks on a plant. We then calculated the total number of hummingbird available flowers for each transect, for each month, by taking the average of the 2 monthly flower counts. We divided these monthly averaged flower counts into low, medium or high resource availability periods based on whether the flower count fell into the lower (0–300 flowers), middle (300–667 flowers) or upper third (above 667 flowers) quantile of all flower counts. These breaks were based on the average flower counts across all years and elevations. These periods generally correspond to before, during, and after the rainy season (Loiselle & Blake 1993; Hilty 1997). We defined the temporal window of our analysis to the timing and location of resources, rather than the calendar month. The distribution of flowering counts was weakly right skewed, with more monthly flower counts in the high resource period (n = 64) than in low resource period (n = 62).

We used observations along the transects to estimate hummingbird species elevation ranges. Upper and lower elevation ranges were based on the 95th quantile of observation records for each bird species (Figure S1). Hummingbird bill morphology was taken from published data sources (Graham et al. 2012). We measured corolla length, defined as the distance from the flower opening to the back of corolla, on at least three plants per species. Wherever possible, we estimated the effective corolla length by cutting open flowers and measuring the corolla length extending back to the flower nectaries. For a minority of species, we were unable to measure floral characteristics, and used values from scaled photographs and local field guides from the UC Davis Herbarium survey of the Maquipucuna Valley (Webster & Rhodes 2001). We removed species from the final dataset if we did not have corolla morphology (n = 13). Only one of the removed plant species (Pitcairnia nigra) was in the top 25 most visited plant species.

To obtain hummingbird-plant interactions, we used time-lapse cameras (Plotwatcher Pros – Day 6) placed 1–3 m from blooming flowers identified during floral transects. Up to 12 cameras were placed during each bi-monthly transect, depending on the availability of accessible flowers. We placed cameras on flowers across a wide variety of morphologies to ensure we captured the broadest floral use. Cameras turned on automatically at dawn and recorded an image every second for at least 1 day. After a maximum of 5 days, cameras were moved to a new set of blooming flowers. We used the computer vision program MotionMeerkat to identify images that contained movement, followed by manual review of these candidate frames to identify hummingbirds (Weinstein 2015). Only hummingbird species whose elevation ranges overlapped with the camera were considered available to interact with a given flower. We excluded one hummingbird from our analysis, Sparkling Violetear (Colibri coruscans), because it only briefly visited our field-site during the year.

Hierarchical bayesian N-mixture model for species interactions

We used an N-mixture model that assumes that there is a true, but partially observed, number of interactions between a given flower and hummingbird species. Due to sampling constraints, field observations will only detect a portion of the true number of interactions within a fixed period (Chacoff et al. 2012). Our approach explicitly models this uncertainty by treating each day of camera filming as an attempt to capture the true daily interaction rate among hummingbirds and flower. In this way, we differentiated the number of interactions per day from the probability of detecting an interaction, given that it occurs. The full model reads, for each observation (Yijkd) of a hummingbird species (i) feeding on plant species (j), during each month (k), on sampling day (d) there is a true number of interactions (Ni,j,k). Our ability to observe this true state is governed by the detectability of each hummingbird species ε(k). The daily visitation rate is a function of the difference in traits between hummingbird bill length (i) and flower corolla length (j), with an interaction term for the resource availability period (low, medium, high) during month (k). The covariate βij is the effect of trait-matching on visitation rates. Since trait-matching is the difference between bill and corolla lengths, a more negative value indicates greater trait-matching. The covariate βij is the effect of increasing resource availability when the difference between bill and corolla lengths is zero. The covariate βij is the interaction between resource availability period (i.e. low, medium and high) and trait-matching. We use the resource availability period as our predictor of visitation rates, rather than the abundance of a given plant species (as in Krishna et al. 2008; Vázquez et al. 2009; Maruyama et al. 2014; Bartomeus et al. 2016), because we believe it is the seasonal change in resource availability which may influence trait-matching. Covariates were considered to have significant biological relevance if their posterior distributions did not overlap with zero. To create posterior distributions, two MCMC chains were run for 300 000 draws. We then sampled 5000 draws, saving every 10th draw, to reduce autocorrelation, to create 500 posterior samples. We parameterised process and observation variance using precision, rather than standard deviation (e.g. precision of 10 is equal to a standard deviation of 0.31).

Observation model

\[ Y_{ijkd} \sim \text{Binomial}(N_{ij,k}, \epsilon_k) \]

Process model

\[ N_{ij,k} \sim \text{Poisson}(\lambda_{ij}) \]
log(λij) = αi + β1i * |Traiti − Traitj| + β2i * Abundancej,k + β3i * Abundancej,k * |Traiti − Traitj|

Priors
logit(ωi) ~ Normal(μω, τω)
αi ~ Normal(μα, τα)
β1i ~ Normal(μβ1, τβ1)
β2i ~ Normal(μβ2, τβ2)
β3i ~ Normal(μβ3, τβ3)
μω ~ Normal(0, 0.386)
μα ~ Normal(0, 0.001)
μβ1 ~ Normal(0, 0.001)
μβ2 ~ Normal(0, 0.001)
μβ3 ~ Normal(0, 0.001)
τω ~ Uniform(0, 10)
τα ~ half − cauchy(0, 1)
τβ1 ~ half − cauchy(0, 1)
τβ2 ~ half − cauchy(0, 1)
τβ3 ~ half − cauchy(0, 1)

To determine whether niche overlap varied among resource periods, we generated 500 daily interaction networks for the high, medium and low resource periods by simulating daily interaction rates from the model’s posterior distributions. For each of these predicted networks we calculated niche overlap among hummingbird species using horns distance (R package bipartite (Dormann et al. 2009)). The virtue of using the model posteriors to generate networks is that we can use the uncertainty in detecting species interactions to estimate the uncertainty in network statistics (Poisot et al. 2015).

RESULTS
We conducted a total of 373 floral transects, recording 17 803 plants in bloom. We recorded 5093 hummingbird observations on these transects, which we used to estimate species elevation ranges (Fig. S1). Elevation ranges were largely constant throughout the year, with a distinct low and high elevation community. Tawny-bellied Hermit was the only species observed in all transects along the elevation gradient.

We placed cameras on 394 flowers in the field for a total of 498 days (c. 6000 recording hours). Our cameras recorded 156 observations of flower piercing, in which hummingbirds bypassed the corolla opening and inserted their bills directly into the corolla base (Table S3). For the most common piercer (Stripe-throated Hermit), the number of piercing decreased, and weakest for the 2300 m to 2500 m elevation transect (Δρ mean = 3.3 mm) (Table S1).

The mean detectability of hummingbird interactions was 23.3% (min = 16%, max = 44%; Table 1). The variance in detectability was low for hummingbird species with many observations, but was high for species observed on less than 10 cameras. The trait-matching covariate (βi) was significant for sixteen of the nineteen hummingbird species. The remaining three species (Green-fronted Lancebill, Andean Emerald, and Green-crowned Brilliant) had inconsistent or no preference for corollas that matched their bill lengths (Fig. 4). We found 156 observations of flower piercing, in which hummingbirds bypassed the corolla opening and inserted their bills directly into the corolla base (Table S3). For the most common piercer (Striped-throated Hermit), the number of observed piercing events during the high resource period (n = 90) was more than twice the number of events during the low resource period (n = 33). This pattern was not consistent for the other species which used piercing less frequently (Fig. S2).

Only three of the nineteen species had significant estimates for the interaction between trait-matching and resource period (βi) (Table 1, Fig. 4). White-whiskered Hermits shifted towards using more poorly matched flowers during periods of high resource availability. Collared Inca and Gorgeted Sunangels shifted towards using more well-matched flowers during periods of high resource availability. The remaining sixteen species showed no significant change in trait-matching between low, medium and high resource availability periods. Model evaluation showed reasonable fit for the majority of species, but under-predicted high daily counts among well-matched hummingbirds and resources (Fig. S3).

The predicted mean niche overlap among hummingbirds was low and broadly overlapping for low, medium and high resource periods (mean: low = 0.23, medium = 0.24, high = 0.25) (Fig. 5). The variance in niche overlap (low = 0.19, medium = 0.18, high = 0.18) was similar among resource periods. Overall, the predicted networks based on the detectability of interactions and the importance of trait-matching did not show a strong change in niche overlap during annual changes in flower abundance and morphology.
Figure 2 Log-transformed available floral resources for hummingbirds along each of the six elevation transects from northwest Ecuador. Transect elevation ranges are shown in the gray headings. Resource availability periods for each transect and month were defined by the upper, middle and lower third quantiles across all monthly flower counts. The blue line is the loess spline trend for each elevation transect throughout the year.

Figure 3 The distribution of hummingbird-visited corolla lengths during high, medium and low resource periods along the six elevation transects in northwest Ecuador. These periods refer to the lower, middle and upper third of flower counts. During elevated resource periods there are greater proportion of shorter corollas, largely due to the mass flowering of sub-canopy trees in the genera Besleria and Palicourea. The more consistent flowering of P. lineata at the highest elevations leads to a less pronounced shift along the 2300–2500 m transect.
Species are sorted by detection probabilities. Significant covariate estimates are indicated in bold. Negative covariates indicate trait-matching is increasing during periods of resource availability. Species frequently have specialised morphology suggesting that this may be a behavioural adaptation to allow for increased foraging breadth (Feinsinger & Colwell 1978).

The premise of trait-matching among interacting species is that species incur a cost in utilising poorly matched resources (Jordano 1987; Bascompte & Jordano 2007; Bartomeus et al. 2016). However, trade-offs are often assumed, rather than tested, and there is evidence for a lack of trade-offs in some cases (Futuyma & Moreno 1988; Wilson & Yoshimura 1994; Cogni et al. 2012; Remold 2012). MacArthur’s adage ‘The jack of all trades is the master of none’ (MacArthur 1972), would lead us to believe that trait-matching among morphological specialists would be the rule among co-occurring species trying to maximise foraging efficiency. However, perceived morphological specialists may act as foraging generalists, often called ‘Liem’s paradox’ (Liem 1973), underlining the importance of monitoring species interactions through time (Olesen et al. 2008; Petanidou et al. 2008; Poisot et al. 2015). Our observed lack of shift by long-billed birds to more abundant short corolla flowers, combined with the tremendous metabolic demand of hovering flight (Altshuler & Dudley 2002), frequent agonistic interactions among individuals (Powers & Conley 1994), and improved nectar extraction rates for well-matched interactions (Rico-Guevara & Rubega 2011; Maglianesi et al. 2014), suggest there is a foraging trade-off for hummingbird with specialist morphologies.

Increased interaction rates among species with well-matched traits has been highlighted in a variety of systems, including hummingbird-plant interactions (Abrahameczyk et al. 2014; Maglianesi et al. 2014; Maruyama et al. 2014; Vizentin-Bugoni et al. 2014), frugivore-plant interactions (Donatti et al. 2011; Dehling et al. 2014; González-Castro et al. 2015), insect-plant interactions (Stang et al. 2009; Kaiser-Bunbury et al. 2014; Szathmary et al. 2016) and marine food-webs (Gravel et al. 2013). Our study is one of the first to evaluate the seasonal changes in trait-matching and available resource morphology. While we found limited seasonal change in trait-matching, there are many examples of seasonal diet switching (Foster 1977; Carnicer et al. 2008; Correa & Winemiller 2014). However, these studies did not explicitly measure the change in trait-matching, limiting our ability to create a general framework for when trait-matching is favoured (D’Andrea et al. 2013; Whitehead et al. 2013).
We expect that the degree of trait-matching is a trade-off between the search time needed to find well-matched resources, vs. the ease of use of poorly matched resources (Connell 1983; Pyke 1984). Multiple mechanisms may shape this trade-off, including the relative quality of resources, the intensity of interspecific competition, and the spatial patterning of resources (Bartomeus et al. 2016). For example, Levey et al. (1984) found that tropical frugivores consumed less preferred fruits when the distance among preferred fruits was experimentally increased. In our system, the pulse of resources are distributed in distinct patches (i.e., sub-canopy trees), such that they can be dominated by relatively

Figure 4 Trait-matching relationship among hummingbirds and plants during periods of low, medium and high resource availability periods from a cloud-forest in northwest Ecuador. Trait-matching is measured as the difference between bill and corolla lengths, therefore a negative slope is indicative of positive trait-matching. Ninety-five percent credible intervals are shown in the shaded regions.
few individuals from aggressive species (Temeles et al. 2004). We suspect that if resources were uniformly distributed across a landscape, it might be impossible to defend all small flower patches, thereby reducing competition, and relaxing the pressure on foraging efficiency (MacArthur & Pianka 1966; Mac Nally & Timewell 2005).

The separation of species niches through trait-matching may help explain the modularity reported in many mutualistic networks (Dalsgaard et al. 2013; Martín González et al. 2015). In general, strong trait-matching will lead to greater specialisation and modularity within assemblages (Carstensen et al. 2016). This modularity may lead to greater isolation among hummingbird-visited plants with different floral morphology; thereby minimising hybridisation, pollen loss and competition for pollinator services (Castellanos et al. 2004; Muchhala & Thomson 2010). In this way, trait-matching can shape the diversity of assemblages, and the potential co-evolution of plant-pollinator interactions (Muchhala & Thomson 2009).

While the potential importance of temporal change on inferring network properties has been extensively discussed (Vázquez & Aizen 2004; Poisot et al. 2015), there have been few datasets with sufficient detail to capture changes in species interactions through time (Petanidou et al. 2008; Olesen et al. 2011). We used time-lapse cameras, computer vision and a hierarchical Bayesian approach to increase sampling and differentiate the uncertainty in detecting an interaction from the underlying probability of interaction among network partners (Bartomeus 2013). Within our dataset, we saw species specific trait-matching relationships and changes through time. Given the idiosyncratic results for individual species, methodological approaches that use aggregated interaction matrices may overlook species-level complexity in network partners (Olito & Fox 2015; Carstensen et al. 2016).

Further evaluation of the importance of trait-matching to the maintenance of biodiversity requires broader-scale studies across evolutionary lineages, species richness and community composition (Dalsgaard et al. 2013; Poisot et al. 2015). There may be reduced trait-matching in young assemblages, due to insufficient time for such adaptations to evolve, or in species-poor assemblages, due to reduced competitive pressure on the efficiency of resource extraction (MacArthur et al. 1972; Costa et al. 2008). For example, Dalsgaard et al. (2016) suggested that the depauperate hummingbird community on Cuba has led to the unusual diversity of nectar-feeding avifauna. This pattern may relate to the density of trait space within assemblages, such that in areas of low functional density, there is weaker advantage for trait-matching (Bartomeus et al. 2016). However, Sazatornil et al. (2016) found evidence for the reverse, in assemblages with a greater proportion of morphological specialists, there was reduced evidence for trait-matching. Whether the importance of trait-matching depends on trait spacing among competitors remains an interesting and open question. By combining observations from multiple sites, mechanistic models of trait-matching, and accounting for the detectability of interactions, we can gain a more detailed insight into why species interactions vary across time and space.

DATA ACCESSIBILITY

Should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository such as Dryad or Figshare and the data DOI will be included at the end of the article.

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AUTHORSHIP

BW, CG developed the conceptual ideas for the MS; BW conducted the analyses; BW and CG wrote the MS.

APPENDICES AND DATA AVAILABILITY

All data, R code, and analysis can be found in reproducible documents at http://bw4sz.github.io/NetworkPredict/.
REFERENCES


SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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