The hummingbird and the hawk-moth: species distribution, geographical partitioning, and macrocompetition across the United States

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ABSTRACT

Macrocompetition –higher taxa suppressing species richness and adaptive radiation of others – exists as a potentially intriguing possibility. We investigate possible evidence for this phenomenon occurring between two convergent nectarivorous families, the hawk-moths (Sphingidae) and hummingbirds (Trochilidae) by searching for geographical partitioning over the continental United States. Using stepwise regression, we tested for latitudinal and longitudinal biases in the species richness (S) of both taxa and the potential role of 10 environmental variables in their distribution pattern. Hawk-moth species richness increases with longitude (eastward-bias) while that of hummingbirds declines (westward-bias). Hawk-moth species richness is positively correlated with higher temperatures overall (especially summer minimums), atmospheric pressure, and summer precipitation; hummingbird species richness is negatively correlated with atmospheric pressure and positively correlated with winter daily maximums. Overall, hawk-moth and hummingbird species richness patterns support the operation of macrocompetition and large scale niche partitioning between the two taxa. Hawk-moth species richness was highest in states with low elevation, summer-time flowering and warm summer nights. Hummingbird species richness is highest in the southwest with higher elevation, more cool season flowering and high daytime winter temperatures. Similar geographic patterning can be seen across the Canada and South America. With this analysis, we see macrocompetition potentially occurring between these two families as two of three of Brown and Davidson (1979) indicators for – niche overlap and geographical partitioning are strongly suggested. We hope that our study helps to further exploration into a potentially undescribed form of competition and the understudied relationship between hawkmoths and hummingbirds.

INTRODUCTION

Of the three main direct ecological interactions – competition, predation, and mutualism – competition is believed to be the most important of the three, accounting for the distribution (Hutchinson 1978), origination (Rosenzweig 1978; Hutchinson 1978; Schluter 2000; Ripa et al. 2009) and extinction of species (Gause 1934). Competition is known to affect small-scale interactions among species and also drives larger scale phenomena. Incumbent replacement… and even various hypotheses on speciation have competition at their core (Rosenzweig and McCord, 1991; Rosenzweig, 1978). Competition is often studied at the local scale, either between individuals within a population mutually suppressing fitness or between populations mutually suppressing population size. Competition may also exist at higher taxonomic levels; if a taxonomic group occupies potential niche space for another taxonomic group, it can prevent an adaptive radiation of the latter. In this form of competition, species richness itself is suppressed rather than fitness or population size. One can think of competition acting on three levels: microcompetition which occurs between individuals and acts on fitness, mesocompetition which occurs between populations and suppresses population size, and macrocompetition which occurs between higher order taxa and suppresses species richness.

Bearing in mind that macrocompetition occurs on different scales from micro- and mesocompetition, both temporal and geographic scales are key. Because macrocompetition suppresses species diversity and the radiation of taxonomic groups, macrocompetition must occur over large geographic scales and at taxonomic levels higher than the species. Because of this link between spatial, temporal, and organizational scales, macrocompetition must be studied at its own appropriate scale. Just as population level mesocompetition is not studied by aggregating individual microcompetitive interactions, macrocompetition cannot be studied

through the aggregation of mesocompetitive and microcompetitive interactions.

A strong analogy can be seen in the field of economics. Two worldviews compete in macroeconomics: microfoundations, in which individual microeconomic interactions are analyzed and then aggregated to understand macroeconomic properties, and the classical aggregate demand--aggregate supply (AD-AS) approach which, as its name suggests, first aggregates the actors into types (home, business, government, etc.) and then studies the interactions among the aggregates. Of these two approaches, AD-AS has arguably yielded the best knowledge in the field compared to microfoundations due to the different scales at which macroeconomics and microeconomics work. As an example, the overall dynamics of the laptop market have less to do with competition between, say, HP and Dell, or even competition between HP and the iPad, and more to do with consumer preferences towards the laptop, tablet, and smartphone markets as a whole. In the same way, when studying macrocompetition, the shared characteristics within each clade and how they affect each clade's ability to exploit various environments is what's most important – not the particuliarities of each species within the clades.

Key to the study of macrocompetition must is how different taxonomic groups interact with each other. Mesocompetition between populations of different taxa has been well-documented. Examples include tadpoles and aquatic insects (Morin et al., 1988) and insect larvae (Mokany and Shine, 2003), granivorous rodents and ants (Brown and Davidson, 1977), granivorous birds and rodents (Brown et al., 1997), frugivorous birds and bats (Palmeirim et al., 1989), insectivorous lizards and birds (Wright, 1980), and insectivorous birds and ants (Haeming 1994, Jedlicka et al. 2006). Competition may even exist between species of separate phyla, such as the competition between scavenging vertebrates and microbes for detritus (Janzen, 1977; Shivik 2006) or vertebrates and fungi for rotting fruit (Cipollini and Stiles 1993; Cipollini and

Levey 1997). Brown and Davidson (1977) identified three key indicators to determine potential intertaxonomic mesocompetition: 1) reciprocal increases in population size when competing species are excluded, 2) shared extensive use of the same particular resource, and 3) partitioning along a geographic or climatic gradient. Having these three criteria met strongly indicate the possibility for inter-taxanomic competition at the mesocompetitive scale. We should expect the same three indicators to be strong signals of macrocompetition with key modifications. Adapting Brown and Davidson's indicators for a macrocompetitive framework, the three indicators become 1) reciprocal increases in species richness and adaptive radiation when competing taxa are excluded, 2) shared extensive use of the same class of resources, and 3) partitioning along geographical and climatic gradients across the shared taxa's range.

Pollination systems provide ample opportunities for inter-taxon competition, particularly systems that include hummingbirds. Studies have investigated the pollination interactions between hummingbirds and skipper (Primack and Howe, 1975) and other butterflies (Thomas et al., 1986), bumblebees (Laverty and Plowright, 1985), and more. Due to their convergent characteristics, interactions between hawk-moths (Sphingidae) and hummingbirds (Trochilidae) seem just as likely. Both groups of animals are highly-specialized nectar feeders and pollinators as adults. They have similar sizes, hover when feeding, and some species in each taxon possess tongues and other features that are often adapted to single species of plants (Johnsgard, 1997; Tuttle, 2007). Despite this remarkable similarity and strong niche overlap, competition between these two families has been seldom investigated. Only Carpenter (1979) explored the possibility of direct competition between hawk-moths and hummingbirds. Her study documented spatial and temporal partitioning between hawk-moths and hummingbirds, hawk-moths dominating *Ipomopsis* feeding sites when first to establish due to overexploitation of nectar resources, and

hummingbirds exhibiting aggressive behaviour towards hawk-moths. The latter point especially suggests hummingbirds perceive hawk-moths as a competitive threat.

Differences in morphology and physiology can lead to broad scale biogeographical patterns (Buckley et al., 2012). With this in mind, we examined and compared species richness of hummingbirds and hawk-moths at the continental scale of the United States with the goal of inferring competition between the families. We seek broad scale geographic and climatic correlations of diversity that might provide insights into the patterns of diversity of hawk-moths and hummingbirds and the possibility of inter-taxon competition shaping the patterns. Do diversity patterns of these two families covary positively or negatively? As nocturnal ectotherms, does hawk-moth diversity increase with summer rain and temperatures? As diurnal endotherms, do hummingbirds gain a competitive edge with colder temperature and cool season flowering? Do hawk-moths suffer more from low oxygen and elevation than do hummingbirds? Ultimately, to what extent can large-scale biogeography provide insights and clues into competition and niche partitioning?

METHODS

Study Families

Hawk-moths, order Lepidoptera, family Sphingidae, and Hummingbirds, order Apodiformes, family Trochilidae, are nectarivores exhibiting morphological hallmarks of convergent evolution. Worldwide, the approximately 953 species of hawk-moths (Kitching, and Cadiou, 2000) are moderate to large sized insects with wingspans that range from 25 to 200 mm (Kitching and Cadiou, 2000) with body weights ranging from 0.1 to 7 g (Janzen 1984). Hawk-moths outside of Smerithini typically possess enhanced proboscides for nectar feeding and water drinking, allowing a longer lifespan than species which survive on fat reserves during their adult

phase of the life cycle (Janzen, 1984). Due to their long lives, hawk-moths may have greater neural capabilities. Locally they seem to know visited and unvisited flowers, over the course of days they seem to efficiently revisit flowers and patches on a regular basis, and over the seasons they exhibit well directed long distance movements and migrations (Janzen, 1984). Hawk-moths have also evolved unique flight skills, including the ability to hover and a capacity for quick, long distance flight (Scoble, 1992). For instance, about half of the hawk-moth species at Santa Rosa National Park in Costa Rica migrate out of the park (Janzen, 1986). Many North America species disperse across continents, though the consistency and regularity of such dispersals are unknown (Tuttle, 2007). Some North American species likely migrate between North and South America as such cross-continental migration is known for many hawk-moths of the Western Palearctic (Pittaway, 1993).

All of the approximately 328 hummingbirds reside in the New World (Schumann, 1999). The family includes the smallest known bird species. Body masses across species range from 2 to 21 g (Schumann, 1999) with wing lengths from 29 to ≥ 90 mm (Johnsgard, 1997). Hummingbirds, like hawk-moths, possess specialized features for nectar-feeding, including elongated bills and extensible bitubular tongues for reaching and extracting nectar. Large breast muscles (30% of body weight) and specialized wings giving them the ability to hover and fly backwards. Hummingbirds are capable of long distance flight, with 13 of the 15 species of the United States exhibiting some degree of long distance migration (Johnsgard, 1997).

Many New World species of flowers exhibit distinct pollination syndromes that favour each family's morphology and behaviour. Moth-pollinated (phalaenophilic) flowers usually open at night and use odour instead of visual cues to attract pollinators, resulting in strongly scented but pale flowers. Furthermore, due to a moth's thin proboscis, the nectar tubes are comparatively

narrow. Hummingbird-pollinated (ornithophilic) flowers, on the other hand, open during the day, are vividly coloured (usually red), and have little to no scent. Nectar tubes are also comparatively wide (Faegri and van der Pijl, 1979). Divergence also occurs in the position of flower sex organs where hummingbirds seem to prefer flowers with exserted sex organs – sex organs extending beyond the corolla – while hawk-moths prefer flowers with inserted sex organs (Kulbaba and Morley, 2008). That being said, there is a general similarity between pollination syndromes of hawk-moths and hummingbirds due to the convergent evolution. Both phalaenophilic and ornithophilic flowers have abundant nectar sources contained deep within long nectar tubes. Visual guides for pollinators are relatively absent in both flower types, with moths using the contours of the blossom as a guide (Faegri and van der Pijl, 1979). As well, both families prefer high sugar and abundant nectar with both families feeding on the other's flowers quite regularly (Cruden et al., 1983; Cruden et al., 1976; Hraber and Frankie, 1989). This shows a high degree of niche overlap and offers opportunities for competition.

Methods

We determined the species richness of hummingbirds and hawk-moths across the continental USA. Using range maps and text descriptions provided by Johnsgard (1997) and Tuttle (2007), we determined the species richness for the 49 states. We used states as our scale of resolution because sufficient finer scale distribution data for hawkmoths does not exist. We included rare native species but excluded species non-native to the United States. We used the centroid of each state as its longitude and latitude. We used these latitudes and longitudes as independent variables and species richness as the dependent variable within a general linear model to test for geographic gradients in the diversity of each family. Once confirmed, we investigated a number of environmental variables as potential determinants of the pattern.

For each state, we investigated its average daily, maximum, and minimum summer and winter temperature; average summer and winter precipitation, along with the difference between the two (winter minus summer) to eliminate any bias due to total rainfall; and average atmospheric pressure. Using the Monthly Station Normals 1971-2000 CLIM 81 from NOAA and averaging across all weather stations within each state, we calculated the mean precipitation and mean daily maximum, minimum, and average temperature per state. Winter variables were calculated by taking the respective means of December, January, and February while the summer variables used June, July, and August. Precipitation was used as a proxy for time of flowering (cool season vs. warm season). Since changes in elevation also lead to changes in both temperature and atmospheric pressure, we used the barometric formula (eq. 1) with the annual average temperature and elevation of the state to determine average atmospheric pressure (Table 1). Mean elevation per state was taken from the 2004-2005 Statistical Abstract of the United States, Section 6.

$$P_h = P_0 e^{\frac{-g*M*(h-h_b)}{R*T}} \qquad (1)$$

General linear modelling was used to determine which variables correlated significantly with species richness. For each family separately, we used a step-wise regression, eliminating at each step the least significant variables based upon their p-values. This left a linear model with the remaining significant variables at a level of $p < 0.05$. As various variables overlapped in terms of information, several different permutations of tests were done. The first permutation used the variables summer daily average temperature, winter daily average temperature, winter precipitation, summer precipitation, and atmospheric pressure. Since the west is drier and has an overall lower amount of precipitation, we ran a second test using the precipitation difference in lieu of winter precipitation and summer precipitation. A third test was done using daily

maximum summer and winter temperatures for hummingbirds and daily minimum summer and winter temperatures for hawk-moths as the two families are diurnal and nocturnal respectively.

While not analysed as extensively, patterns of hawkmoth diversity at the county level in Oklahoma and the province level of Canada, and hummingbirds across Canada, Mexico, and South America also proved instructive. Taking advantage of sufficiently detailed data, we can provide figures for the diversity of hawkmoths at the county level within Oklahoma and province level in Canada, and for hummingbirds across Canada, Mexico and South America.

Our analyses and data pooling have limitations. Firstly, correlations will not necessarily illuminate causation. Yet, given the degree to which hawk-moths and hummingbirds have been ignored as potential shapers of each other's biodiversity and distributions, correlations will shed light on some of our hypotheses and suggest new ones. Secondly, using states as our unit of replication is geographically crude; they vary in size by more than two orders of magnitude, have diverse and irregular shapes, and adjacent states will have some degree of spatial autocorrelation. A more fine-grained and detailed level of division, such as the county, or the use of GIS data would be preferable, and in many cases possible for hummingbirds. Unfortunately, hawk-moth diversity and distribution data are as crude and, in many cases, cruder than the geographic data that we have used. Fine grain data on hawk-moth species' ranges and presence/absence are deficient throughout the world and digital range maps are scarce to non-existent. We feel our scale best balances the need for accurate data and diverse sampling units. We have high confidence in state-wide inventories of hawk-moths but not those at any smaller scale with perhaps a few notable exceptions, namely county records from the Oklahoma Biological Survey. Perhaps, intriguing results will inspire more detailed interest and work. Thirdly, due to the irregularities of species boundaries, states, especially those along the border with Mexico, could

contain species with well-established populations that occupy just a fraction of the state. While this inflates the numbers of species within the state, any boundary drawing would necessarily have this problem. We felt it best to accept the current haphazard sizes and irregularities of states rather than create more regular spatial sampling schemes that would amplify hawk-moth presence/absence uncertainties.

RESULTS

Fifteen hummingbird species and 101 hawk-moth species inhabit the continental United States. Figures 2a and 2b show the species richness of hawk-moths and hummingbirds, respectively, in the United States and Canada by state, province, and territory. Inspection of these graphs reveals that hummingbird species increase from north to south and from east to west. Hawk-moth species likewise increase from north to south (Figure 2a). In contrast to hummingbirds, hawk-moth diversity increases from west to east. The result of the latitudinal and longitudinal GLM confirm the directional bias seen on the map as seen in Table 2. For hawk-moths, the relationship with geography is S = 115.546 – 1.301*LAT + 0.264*LONG, r^2= 0.464; for hummingbirds, S = -2.669 – 0.143*LAT – 0.116*LONG, r^2= 0.454. In summary, hummingbird diversity peaks in the Southwestern United States, while hawk-moth richness peaks in the Southeastern United States.

We examined the association of selected environmental variables with the diversities of hawk-moths and hummingbirds. Hawk-moth species richness increases with summer precipitation and summer daily average temperatures (hawk-moth S = -7.7010 + 0.1157*SUM.PRECIP + 1.4704*SUM.AVG, r^2= 0.6448, AIC=169.37; Table 3). Hummingbird species richness decreases with winter and summer precipitation and increases with winter daily average temperature (hummingbird S = 8.21519 – 0.02111*WINT.PRECIP –

0.05203*SUM.PRECIP + 0.24945*WINT.AVG, r^2= 0.6518, AIC=47.64; Table 3). A second test was run as described in the Methods, with precipitation difference in lieu of average winter and summer precipitation. For hawkmoths, the relationship now showed an increase with winter daily average temperature and atmospheric pressure and a decrease with precipitation difference – a preference for summer rains – (*S* = -20.73112 – 0.09384*PRECIP.DIFF + 0.87037*WINT.AVG + 57.24767*ATM, r^2=0.6187, AIC=173.67; Table 4); hummingbird species richness now showed a positive correlation with winter daily average temperature and a negative correlation with atmospheric pressure (*S* = 31.0435 + 0.1767*WINT.AVG – 30.6302*ATM, r^2= 0.5149, AIC=62.96; Table 4). The third test, which included the respective minimum and maximum temperatures, showed similar correlations for hummingbirds as the second test but for new coefficients (*S* = 28.5440 + 0.1644*WINT.MAX – 28.9777*ATM, r^2= 0. 5148, AIC=173.8; Table 5) but showed that hawkmoths were only significantly correlated with summer daily minimum temperature (hawk-moth *S* = -5.9047 + 1.8898*SUM.MIN, r^2= 0. 6035, AIC=62.97; Table 5). In summary, hawk-moth diversity increases in states with higher summertime precipitation and temperatures, particularly the minimum temperature (consistent with nocturnal activity), and states with overall low elevations. Hummingbird diversity is higher in states with higher wintertime temperatures, particularly the winter highs (consistent with diurnal activity), and states with higher elevation.

DISCUSSION

In this study, we investigated broad scale geographical patterns of species richness of two key, convergent, yet phylogenetically distant, pollinator families: hawk-moths and hummingbirds. We used data from the literature to look for broad-scale ecological correlates of the species richness of each taxon to infer possible causes of the distribution patterns we found.

Our primary objective was to identify evidence to support or refute family-level inter-taxon interactions, specifically competition, and niche partitioning. We believe the analyses generally support the hypothesis of inter-taxon competition, but with caveats. Below we present our interpretation of the data in support of inter-taxon competition and niche partitioning along with the limitations of the data and our analyses. Though rough, we feel that our study highlights and illuminates on an important yet understudied and underappreciated relationship.

Basic Geography

Of the 15 hummingbird species and 101 hawk-moth species in the US, there is a clear and opposite directional bias in species richness of these two families. The vast majority of hummingbird species are found in the western United States, with only 1 species found east of the Rock Mountains. This result is generally consistent with the expectation that species diversity should be greater in mountainous areas due to habitat heterogeneity and reproductive isolation (though it must be said not as extreme as having only one species in the eastern United States). The distribution of hawk-moths on the other hand offers some striking and initially counter-intuitive patterns. Despite their relatively large size and habitat heterogeneity, western states are conspicuously depauperate in hawk-moth species. States on the eastern seaboard just a fraction of the size of California have much higher hawk-moth diversities. Similar diversity asymmetries appear when noting Maine's (extreme northeast) high diversity in contrast to low diversity in the state of Washington (far northwest). Even neighboring states show this pattern with North Dakota having over 25% more hawk-moth species than Montana despite being smaller in area, sharing a biome, and offering much less environmental heterogeneity.

This directional bias seems to pervade all of North America, from Canada to Mexico. Looking at Canada, we see that only one species of hummingbird exists east of the province of

Alberta, while hawk-moths are quite more numerous in eastern Canada with tiny Prince Edward Island having the same number of species as British Columbia. In Mexico, it is harder to see such a clear delineation of geographical biases, largely due to the fact that Mexico has proportionally less flat and low-lying area compared to the United States and Canada as well as the fact that hawkmoths species richness by Mexican state is unavailable. Still looking at the figures, they tantalize at the phenomenon seen in the United States and Canada. Looking at the Yucatan, hummingbirds are depauperate compared to close-by and neighboring states. Each state (Yucatan, Campeche, and Quintana Roo) has only 9 species each – 10 combined – compared with 14 in neighboring Tabasco, 20 in Michoacán, and 26 in Guerrero. Similarly, there are 133 hawkmoths present in Veracruz alone compared to 120 in Nayarit, Jalisco, Colima, Michoacán, Oaxaca, and Guerrero combined.

Just like North America, South America shows hints of having the same directional bias of hawkmoths in the east and hummingbirds in the west. It is well known that hummingbird species richness is highest in the Andes in western South America (Johnsgard, 1997; NatureServe, 2010). For example, Ecuador has approximately twice as many species as Brazil while Chile has a higher hummingbird species richness per area than Argentina despite having fewer species overall. Though the data are significantly less comprehensive, our search seem to indicate that South American hawkmoths show a geographical pattern similar to their North American counterparts, with species richness highest in places like French Guiana, Argentina, Bolivia, and Venezuela (CATE, 2010). This information is highly suggestive of the opposing roles that climate and topography seem to play in the continental species distributions of hawk-moths and hummingbirds.

Climate Analysis

According to our regression analysis, the realized niche of hawkmoths is an area of high temperatures – especially high summer minimums – high summer precipitation, and high atmospheric pressure. Being nocturnal ectotherms, hawkmoths should reach relatively greater densities in areas with higher summer temperature minimums that allow them to maintain body temperature. Study along a mountainous gradient showed that hawkmoth feeding and pollinating activity fell off once summer minimums reached below 15ºC in mountainous areas (Harlington, 1968; Cruden et al., 1976). As they are active during the summer, they should also attain greater densities in areas with greater summer rains that promote summer flowering nectar sources. In addition to high temperatures, hawkmoths rely on high oxygen density to maintain function. Their tracheal respiratory system requires diffusion of O_2 and CO_2 into and out of spiracles located on the exoskeleton. This system, while extremely efficient at low elevations with high atmospheric pressure is relatively inefficient at high elevations with low atmospheric pressure. Adult insects, as shown by a study with the tobacco hornworm, *Manduca sexta*, are smaller when reared under hypoxic conditions (Harrison et al., 2010). And, smaller size is not favorable for hawk-moths that must maintain thoracic heat for flight (Dorsett, 1962). These characteristics make mountainous areas highly unattractive to hawkmoths. When it comes to hawkmoths, their realized niche nicely overlaps with their assumed fundamental niche.

The realized niche of hummingbirds, on the other hand, is an area of high winter temperatures and lower atmospheric density according to our analysis. The negative correlation between hummingbird diversity and atmospheric density agrees with other studies. Hummingbird richness in the Americas is highest in the 1800 to 2500m range in the tropical Andes (Schuchmann, 1999) and highest in southwestern United States between the 1500-1800m (Wethington et al., 2005). Their adaptations make them able to survive in their realized niche.

Being endotherms, hummingbirds are able to maintain a consistent body temperature. The respiratory system of hummingbirds maximizes the intake of O_2, and correcting for body size, hummingbirds have the largest heart, fastest heart and breathing rates, and densest erythrocyte concentrations among all bird families (Johnsgard, 1997). For these reasons, hummingbirds can maintain a steadier metabolic rate when at higher elevations. For example, *Colibri coruscas* was shown to increase oxygen consumption by only 6 to 8% when hovering under hypoxic conditions equivalent to an altitude of 6000m (Berger, 1974). These physiological adaptations allow hummingbirds to survive at higher elevations and cooler areas, a likely result of having undergone radiation in these areas (McGuire, 2014).

A species' adaptations could be thought of as evolutionary technologies – tools that allow it to exploit environments and resources. As different evolutionary technologies differ in the method of resource exploitation as well as the costs that come with these technologies, these technologies have to shape the fundamental and realized niches of species. It is clear that hawk-moth specializations give them an advantage when living in areas of warm growing season flowering that are low in elevation and oxygen rich while hummingbird specializations give them an advantage in areas of cooler growing season flowering that are high in elevation and relatively oxygen poor. In fact, studies have shown hummingbirds to be better pollinators than insects in the cloudy, windy, and rainy conditions often found at high elevations (Cruden, 1972). That being said, hummingbirds should have a fundamental niche similar to hawkmoths. Though endotherms, hummingbirds are extremely small and quite easily lose heat. In fact, many hummingbird species undergo a nightly torpor to conserve energy. Moreover, though suffering only a small uptick in energetic costs at higher elevations, hummingbirds are still more efficient at lower elevations. Furthermore, many hummingbird species are migratory, only active in the

United States during summer like hawkmoths. Altogether, their fundamental niche should be equivalent with hawk-moths – high temperature, high precipitation, low elevation areas. This raises the question why do hummingbird's fundamental and realized niche do not match up? Fundamentally, *why only one hummingbird species east of the Rocky Mountains*?

Whither Macrocompetition?

Hummingbirds and hawkmoths are two phylogenetically distant, yet morphologically convergent families of nectarivores. Both families display the unique adaptation of the ability to hover while feeding along with long probosces and tongues often adapted for specific flowers. This allows them to exploit efficiently the same class of flowers: ones with deep-lying, sugar-rich, and abundant nectar sources such as Ipomopsis, Nicotiana, Aquilegia, Merremia, etc. (Cruden et al., 1983; Carpenter, 1979; Kessler et al., 2010; Aigner and Scott, 2002; Fulton, 1999; Wilmott and Burquez, 1996). Furthermore, our analysis shows that they exhibit a strong degree of geographical partitioning, most likely due to climatic and environmental variables. These two lines of evidence cover indicators 2 and 3 respectively of Brown and Davidson's criteria for competition and are highly suggestive of potential inter-taxonomic macrocompetition resulting from each family's comparative advantage. That hawk-moths may contribute to an unusually low diversity of hummingbirds in the east and vice-versa in the west remains an open but intriguingly viable hypotheses.

Determining whether the first indicator for macrocompetition applies to our two study families is quite tricky. Brown and Davidson used experimental enclosures to selectively remove rodents or ants to see whether the reciprocal species' populations would increase. Experimentally excluding our families from Texas and seeing if the other radiates would certainly be an intriguing study but is unlikely to gain NSF approval especially in this current political climate.

Fossil and phylogenetic evidence of hawkmoths is also lacking, not allowing for comparisons of evolutionary history. In lieu, other lines of evidence may point to potential competition between the two, specifically that hawkmoths competitively exclude hummingbirds in their optimal fundamental niche space and that hummingbirds are able to radiate extensively only in areas of few hawkmoth species. F. Lynn Carpenter (1979) observed hawk-moths and hummingbirds at an *Ipomopsis* feeding site, finding that hawk-moths leave reduced feeding opportunities for hummingbirds and typically dominated this site. Other studies seem to show flowering plants favouring hawkmoths when it comes to pollination. *Nicotiana attenuata* is seems to favor hawk-moths over hummingbirds, only switching morphology to an ornithophilic syndrome when being predated upon by hawkmoth larvae (Kessler et al., 2010). As well three species of *Calliandra* found in Mexico at low-elevations show adaptations to hawkmoth pollination, but only one species found in the eastern Andes at high elevations shows adaptation to hummingbird pollination as it is (Cruden et al., 1976; Nevling and Elias, 1971). The evidence hints to the possibility that hawkmoths are better competitors and pollinators compared to hummingbirds; it could be that hummingbirds are generally ill-equipped with their specific nectarivorous evolutionary technologies to invade the niche space of hawk-moths. In a manner specific to incumbent replacement, only with the rise of mountains, in which hawk-moths are ill-adapted to live, did a niche space open up for hummingbirds of which to take advantage and radiate to greater species richness.

Another clue that could shed light on the possibility of macrocompetition between hummingbirds and hawk-moths is that the evolution and distribution of nectar feeding bats in the family Phyllostomidae. These bats use the same class of resources, taking from flowers with similar – if not higher – amounts of sugar and nectar to those pollinated by hawkmoths and

hummingbirds (Cruden et al., 1983). The biogeography of these bats show a similar patterning to hummingbirds existing primarily in tropical regions (none inhabit temperate North America) with species richness highest in the Andes; furthermore, phylogeny shows they underwent a radiation in the mid-Miocene around the same time as the hummingbird radiation. Though diversifying in a similar manner to hummingbirds, there are fewer species – and fewer true nectarivores – of these bats than hummingbirds and hawkmoths. In fact, there are only sixteen genera – which contain about 38 species – that are adapted to nectar feeding (Fleming et al., 2009). This may be due to facing competition from both hummingbirds and hawkmoths for available niche space. These nectarivorous Phyllostomidae bats show a similar pollination syndrome to hawkmoths – coming out at night to feed and relying on scent to guide them to flowers instead of visual color cues (most flowers are white) – with some plant species relying on both for pollination (Hernandez-Montero and Sosa, 2015). It could be that bats are constrained by hawkmoths at low-lying elevations and hummingbirds at higher elevation, severely restricting their potential niche space to high-elevation areas at night, suppressing their species richness to severely low levels.

We realize that much of the evidence for our hypothesis of hawkmoths outcompeting hummingbirds, and consequently the first indicator of intertaxanomic competition, is circumstantial. Much more evidence, particularly fossil and phylogenetic evidence, will be needed to confirm or reject the hypothesis. That said, the second and third indicators still remain. All combined, the evidence for macrocompetition between hawkmoths and hummingbirds is quite tantalizing. This all but ignored pollination system is ripe with the potential to lead to deep insights into the eco-evolutionary processes that shape the natural world. Even local, mesocompetitive studies on smaller scales will bring evidence that could explain the relationship

between mounds upon mounds of evidentiary fruit. Looking more generally, we hope our analyses inspire further study into local and even continent-wide distributions and niche partitioning. The possibility of macrocompetition remains alive.

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BIOSKETCHES

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Table 1: State, hawk-moth and hummingbird species richness, and environmental variables. Temperature is in Celsius, Precipitation is in millimetres, and Atmospheric Pressure is in atms.

State	Hawk-moth S	Humming-bird S	Wint Precip	Sum Precip	Precip Diff	Wint Max	Wint Avg	Wint Min	Sum Max	Sum Avg	Sum Min	ATM
AL	44	1	134.59	113.82	20.77	14.14	7.82	1.48	32.09	25.89	19.66	0.982
AK	6	1	85.76	76.61	9.14	-6.73	-10.73	-14.75	17.3	12.27	7.21	0.93
AZ	36	13	32.2	36.31	-4.1	14.94	7.29	-0.38	34.98	26.32	17.62	0.863
AR	39	1	100.03	90.29	9.74	10.94	5	-0.96	32.32	26.05	19.76	0.977
CA	30	7	110.28	6.09	104.19	14.17	8.2	2.19	30.08	21.79	13.47	0.9
CO	31	4	19.36	46.35	-26.99	4.25	-3.61	-11.5	27.51	18.51	9.47	0.777
CT	37	1	98.45	108.24	-9.79	3.08	-2.17	-7.45	26.78	20.66	14.51	0.982
DE	35	1	86.5	102.13	-15.63	7.17	2.19	-2.81	29.2	23.56	17.9	0.998
FL	54	1	75.64	178.19	-102.56	21.81	15.71	9.58	32.59	27.37	22.12	0.996
GA	44	1	116.66	116.22	0.44	14.79	8.41	2	31.94	25.87	19.76	0.979
ID	20	4	46.68	25.47	21.21	1.96	-3.24	-8.46	27.83	18.4	8.95	0.831
IL	42	1	55.99	98.47	-42.47	2.5	-2.3	-7.12	29.12	23.04	16.94	0.978
IN	38	1	65.26	103.02	-37.77	2.97	-1.73	-6.46	28.54	22.51	16.44	0.975
IA	32	1	26.11	110	-83.89	-0.82	-5.93	-11.08	28.19	22.09	15.95	0.96
KS	30	1	23.47	93.04	-69.57	6.22	-0.39	-7.03	31.79	24.73	17.64	0.93
KY	40	1	98.44	104.82	-6.38	7.67	2.14	-3.4	30.08	23.74	17.38	0.973
LA	39	1	135.4	126.52	8.88	16.21	10.4	4.56	32.8	27.33	21.82	0.996
ME	34	1	83.85	92	-8.16	-1.85	-7.77	-13.71	24.29	17.97	11.62	0.978
MD	36	1	83.04	99.11	-16.07	6.86	1.82	-3.25	29.22	23.33	17.4	0.987
MA	38	1	97.54	99.38	-1.84	2.98	-2.16	-7.33	26.17	20.37	14.54	0.982
MI	36	1	47.76	83.59	-35.83	-1.23	-5.7	-10.18	25.45	19.1	12.73	0.967
MN	32	1	19.25	100.89	-81.64	-5.38	-10.87	-16.39	25.91	19.56	13.18	0.956
MS	43	1	137.24	108.46	28.77	13.94	7.93	1.89	32.41	26.44	20.45	0.989
MO	43	1	57.63	98.66	-41.03	5.62	-0.02	-5.69	30.52	24.22	17.89	0.971
MT	24	4	18.57	45.2	-26.63	0.6	-5.45	-11.53	26.82	18.01	9.17	0.881
NE	28	1	14.9	82.44	-67.54	2.93	-3.6	-10.16	29.66	22.4	15.12	0.909
NV	17	5	21.08	13.49	7.59	7.68	0.68	-6.35	31.1	21.19	11.24	0.817
NH	35	1	83.24	101.57	-18.33	-0.65	-6.48	-12.34	24.95	18.4	11.83	0.963
NJ	37	1	90	108.56	-18.56	5.24	0.21	-4.84	28.19	22.31	16.41	0.991
NM	34	9	17	53.38	-36.39	10.37	1.95	-6.5	30.47	21.6	12.71	0.812
NY	39	1	72.26	98.26	-26	0.9	-4.05	-9.02	25.86	19.8	13.72	0.964
NC	39	1	101.54	119	-17.46	11.12	4.98	-1.19	29.72	23.83	17.92	0.975
ND	33	1	11.43	67.58	-56.15	-5.53	-11.09	-16.67	26.75	19.42	12.06	0.931
OH	38	1	64.75	100.63	-35.87	3	-1.69	-6.4	27.81	21.69	15.54	0.969
OK	32	1	46.32	82.31	-35.99	10.48	3.78	-2.95	33.24	26.51	19.75	0.954
OR	19	5	127.35	24.53	102.81	6.64	1.99	-2.7	26.44	17.77	9.08	0.885

PA	39	1	74.75	104.01	-29.26	3.05	-1.9	-6.87	27.1	20.7	14.26	0.96
RI	38	1	103.84	90.66	13.18	4.25	-0.26	-4.79	25.44	20.6	15.73	0.993
SC	40	1	104.4	123.67	-19.27	14	7.62	1.21	31.7	25.79	19.85	0.987
SD	24	1	12.18	69.63	-57.45	-0.63	-6.74	-12.88	28.49	21.06	13.6	0.922
TN	41	1	119	107.94	11.06	9.34	3.55	-2.27	30.34	24.11	17.84	0.968
TX	59	10	50.94	70.98	-20.05	15.86	8.87	1.85	33.94	27.39	20.81	0.941
UT	22	5	29.05	22.87	6.18	4.43	-2.13	-8.71	30.13	20.79	11.43	0.798
VT	34	1	77.91	108.82	-30.91	-1.36	-7.11	-12.87	24.99	18.51	12.01	0.963
VA	37	1	82.74	99.64	-16.89	8.31	2.51	-3.32	29.18	23.01	16.82	0.966
WA	18	4	145.34	34.23	111.11	5.26	1.61	-2.06	24.96	17.77	10.54	0.939
WV	35	1	85.44	111.39	-25.95	5.48	-0.12	-5.74	27.49	21.09	14.67	0.946
WI	37	1	30.44	104.35	-73.91	-2.99	-8.21	-13.46	25.82	19.6	13.36	0.962
WY	27	3	15.14	34.07	-18.93	1.14	-5.8	-12.76	26.93	17.8	8.64	0.779

Table 2: GLM of Latitude and Longitude per state with species richness per family

Family	**S**	**Latitude**	**Longitude**
Sphingidae	101	-1.301[a]	0.264[c]
Trochilidae	15	-0.143[a]	-0.116[a]

a: $p<0.001$, b: $p<0.01$, c: $p<0.05$

Table 3: Coefficients and the total R^2 and AIC for each family's final linear model of Daily Average Winter and Summer Temperature, Winter and Summer Precipitation, and Atmospheric Pressure. N/A signifies the lack of the variable in the final model.

Family	**Summer Daily Average**	**Summer Precipitation**	**Winter Precipitation**	**Winter Daily Average**	**R^2**	**AIC**
Sphingidae	1.4704[a]	0.1157[a]	N/A	N/A	0.6448	169.37
Trochilidae	N/A	-0.05203 [a]	-0.02111[b]	0.24945[a]	0.651	47.64

a: $p<0.001$, b: $p<0.01$

Table 4: Coefficients and the total R^2 and AIC for each family's final linear model of Daily Average Winter and Summer Temperature, Precipitation Difference, and Atmospheric Pressure. N/A signifies the lack of the variable in the final model.

Family	**Winter Daily Average**	**Atmospheric Pressure**	**Precipitation Difference**	**R^2**	**AIC**
Sphingidae	0.87037[a]	57.24767[a]	-0.09384[a]	0.6187	173.76
Trochilidae	0.1767[a]	-30.6302[a]	N/A	0.5149	62.96

a: $p<0.001$

Table 5: Coefficients and the total R^2 and AIC for the final Sphingidae linear model of Daily Minimum Winter and Summer Temperature, Winter and Summer Precipitation, and Atmospheric Pressure and final Trochilidae linear model of Daily Maximum Winter and Summer Temperature, Winter and Summer Precipitation, and Atmospheric Pressure. N/A signifies the lack of the variable in the final model.

Family	**Winter Daily Maximum**	**Atmospheric Pressure**	**Summer Daily Minimum**	**R^2**	**AIC**
Sphingidae	N/A	N/A	1.890 [a]	0.6035	173.8
Trochilidae	0.1644[a]	-28.9777[a]	N/A	0.5148	62.97

a: $p<0.001$, b: $p<0.01$

Table 6: Linear model of Latitude and Longitude with species richness per insect family

Family	**S**	**Latitude**	**Longitude**
Acrididae[3]	215	-0.722	-1.165[a]
Hesperiidae[2]	216	-1.963[b]	-0.114
Libellulidae[3]	109	-1.130[a]	0.206[b]
Nymphalidae[2]	166	0.379	-0.367[b]
Papilionidae[2]	24	-0.126[b]	-0.104[a]
Riodinidae[2]	23	-0.270[b]	-0.078[b]
Saturniidae[1]	69	-0.798[a]	0.035

a: $p<0.001$, b: $p<0.01$

1: closely related by phylogeny, 2: similar in morphology and functional type, 3: distant in phylogeny, different in morphology

Table 7: GLM of Latitude and Longitude with species richness per bird family

Family	**S**	**Latitude**	**Longitude**
Accipitridae[3]	23	-0.142[b]	-0.084[a]
Anatidae[3]	47	-0.093	0.012
Caprimuglidae[1]	8	-0.139[a]	-0.018[b]
Corvidae[3]	18	0.009	-0.111[a]
Emberizidae[2]	42	-0.035[a]	-0.177[a]
Hirundinidae[2]	8	0.077[b]	-0.028[b]
Icteridae[2]	21	-0.167[b]	-0.069[b]
Parulidae[2]	51	-0.128	0.313[a]
Picidae[2]	23	-0.130[b]	-0.087[a]
Turdidae[2]	15	0.128[b]	-0.044[a]
Tyrannidae[2]	34	-0.059	-0.210[a]
Vireonidae[2]	12	0.009	-0.015

a: $p<0.001$, b: $p<0.01$

1: closely related by phylogeny, 2: similar in morphology and functional type, 3: distant in phylogeny, different in morphology

Fig. 1 (a) *Macroglossum stellatarum*, the Hummingbird Hawk-moth, hovering by lavender flowers (b) *Amazilia tzacatl*, the Rufous-tailed Hummingbird, feeding in Costa Rica. As seen in the image below, hawk-moths have extremely long extensile probosces for collecting nectar and the ability to hover in front of flowers. Convergent features are seen in the image of the hummingbird below with long bills and extensile tongues and the ability to hover. Image of *M. stellatarum* by Thorsten Denhard, CC-BY-SA-3.0. Image of *A. tzacatl* by T. R. Shankar Rama, CC-BY-SA-4.0

Fig. 2 Species richness per state, province, and territory of (a) hawk-moths (order Lepidoptera, family Sphingidae) and (b) hummingbirds (order Apodiformes, family Trochilidae) in the United States and Canada. A greater intensity of colour reflects a greater species richness proportional to the highest species rich state/province/territory per family. As one can see, hawk-moths are more species rich in the eastern half of the northern North American continent while hummingbirds are more species rich in the western half of the northern North American continent. Both species show increasing species richness moving from north to south.

Fig. 3 A scatterplot of each states representative average daily July temperature in Celsius and proportional species richness of (a) hawk-moths and (b) hummingbirds. Both plots show a positive correlation of species richness with temperature, indicating that both Families respond in a similar manner to temperature.

Fig. 4 A scatterplot of each states average atmospheric pressure in Celsius and proportional species richness of (a) hawk-moths and (b) hummingbirds. The correlation between hawk-moths and atmospheric pressure (a) is positive while the correlation between hummingbirds and atmospheric pressure (b) is negative, indication that atmospheric pressure has contrasting effects on the Families.

Fig. 1a

Fig. 1b

Fig. 2a

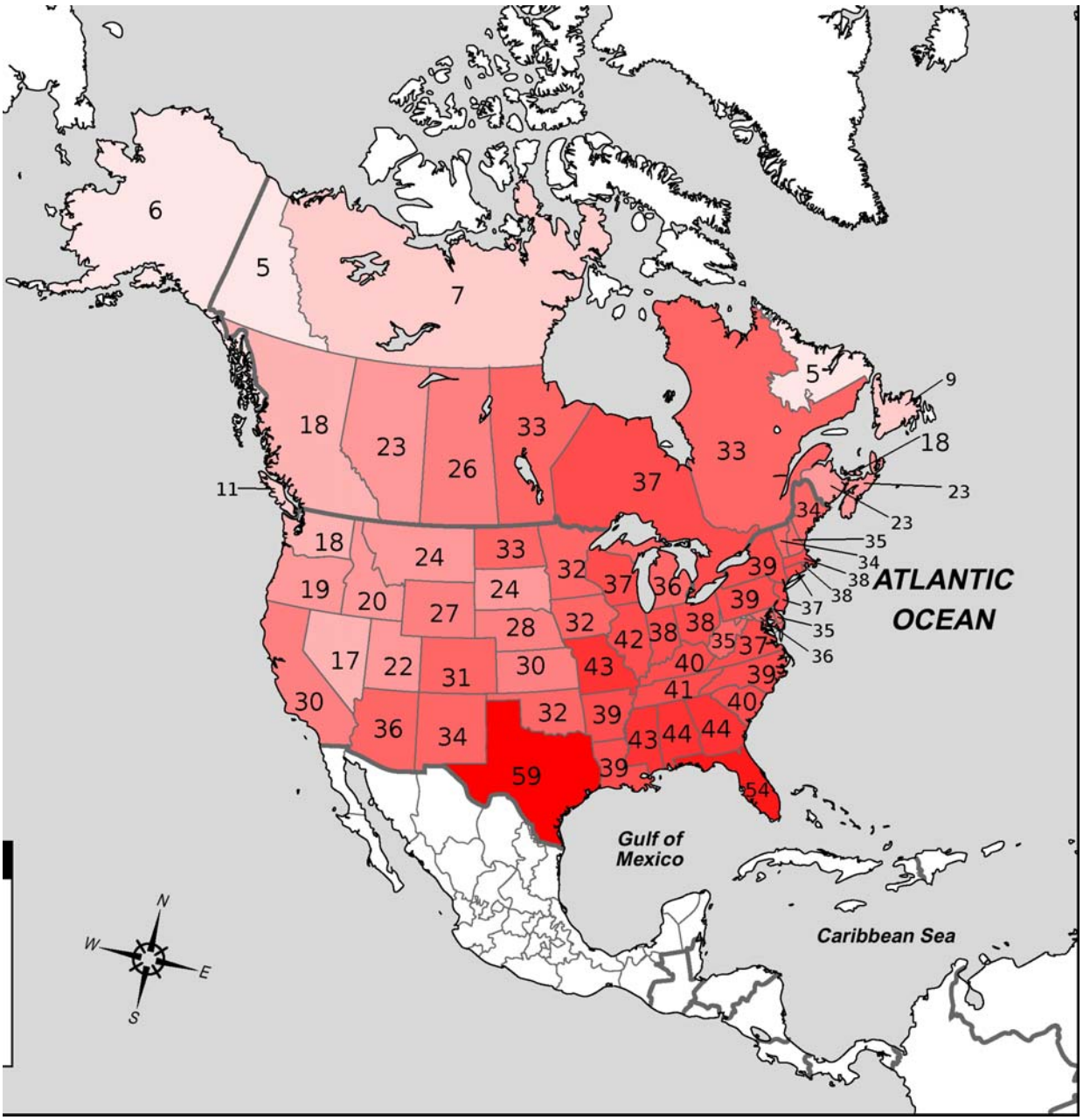


Fig. 2b

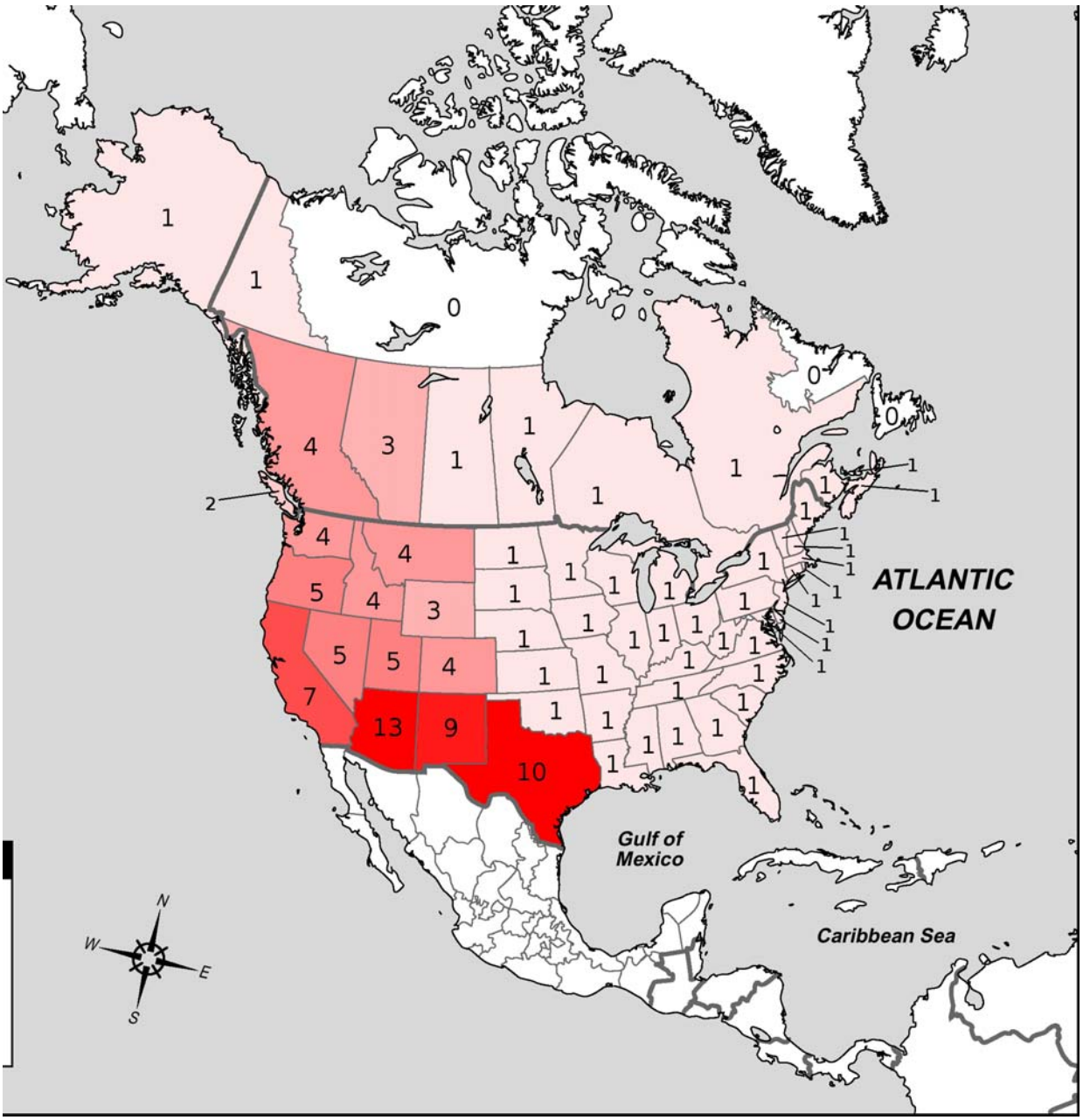


Fig. 3a

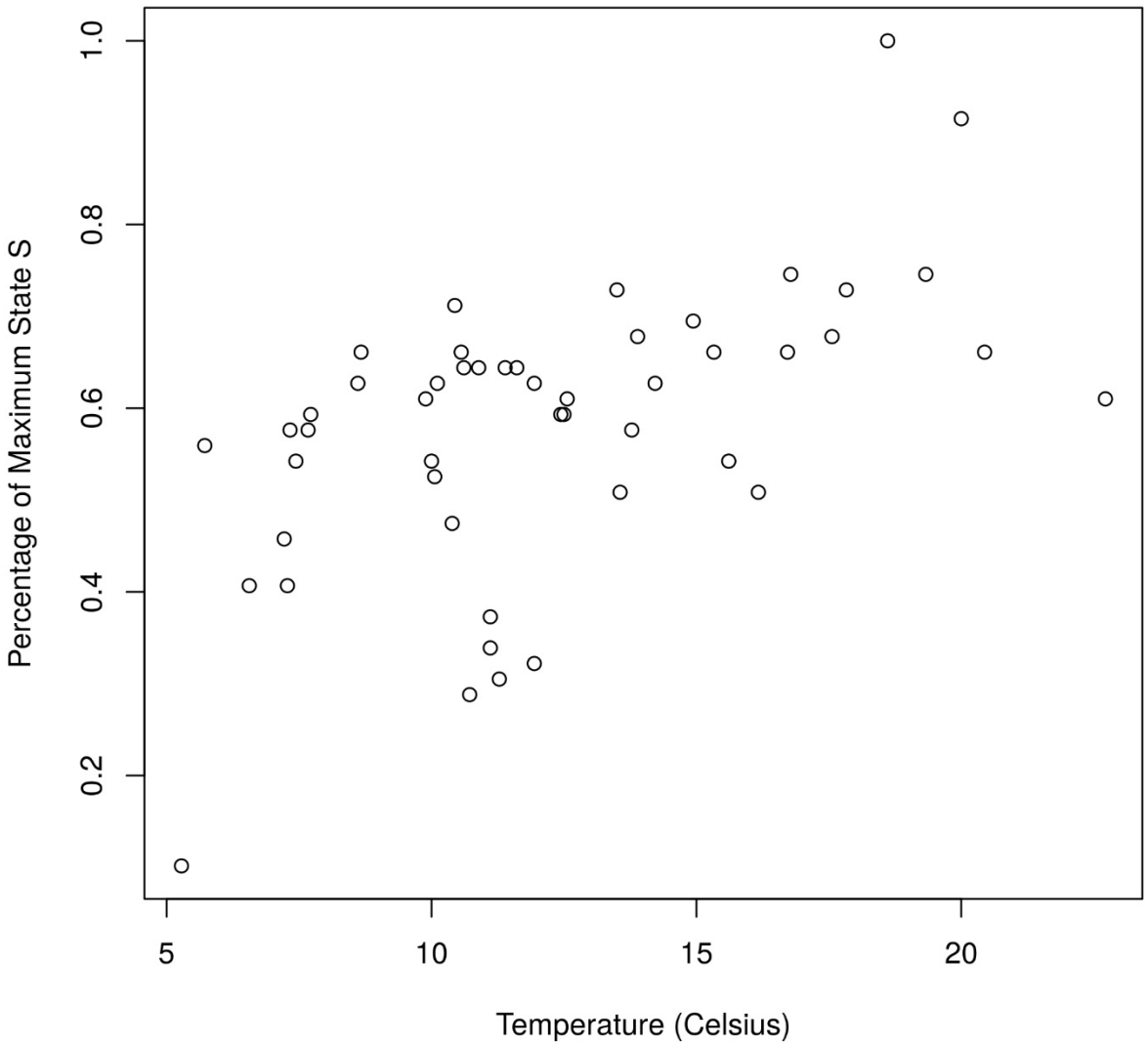
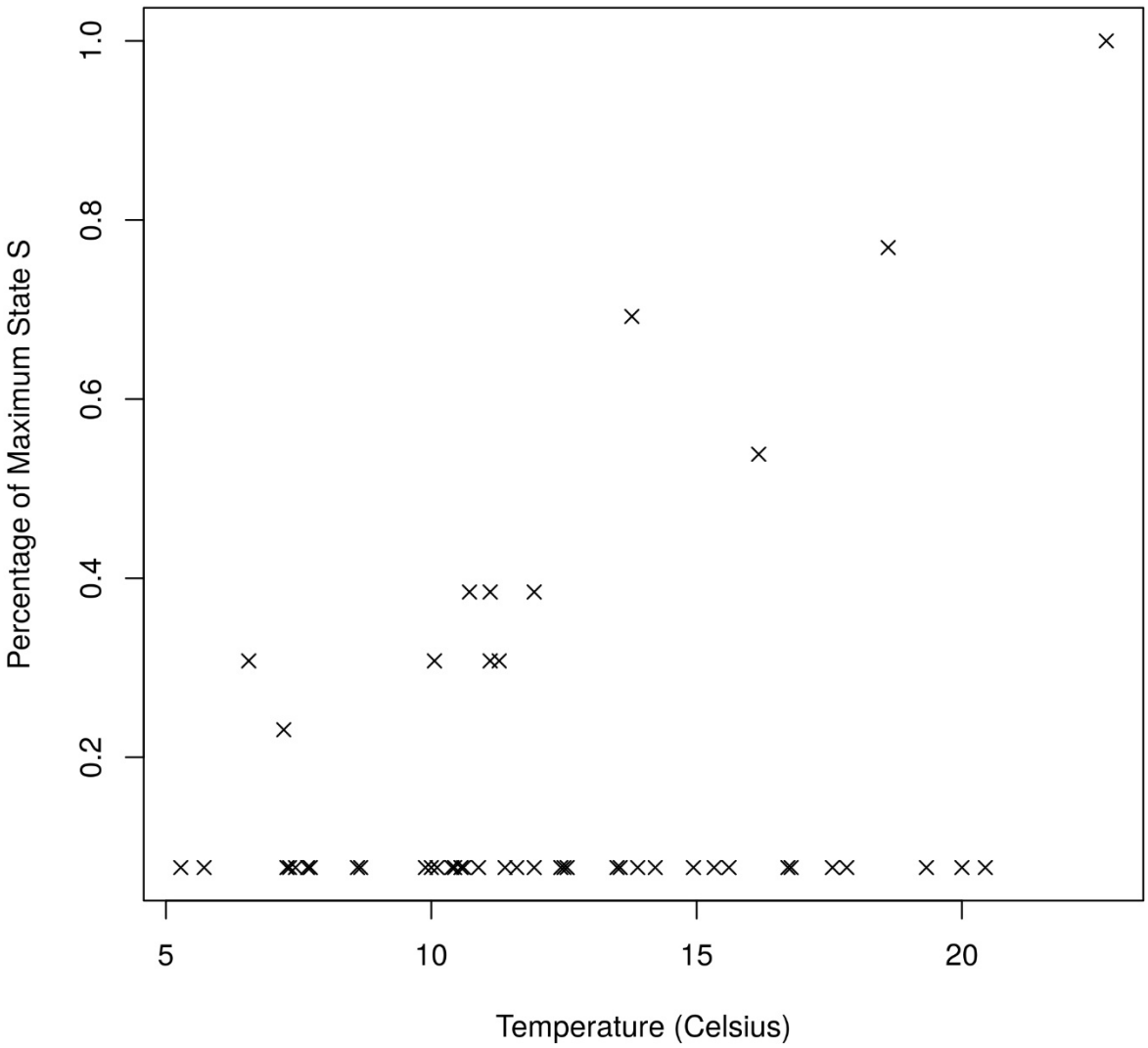

Percentage of Maximum State S
0.2
0.4
0.6
0.8
1.0
5
10
15
20
Temperature (Celsius)

Fig. 3b


Percentage of Maximum State S
0.2
0.4
0.6
0.8
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10
15
20
Temperature (Celsius)

Fig. 4a

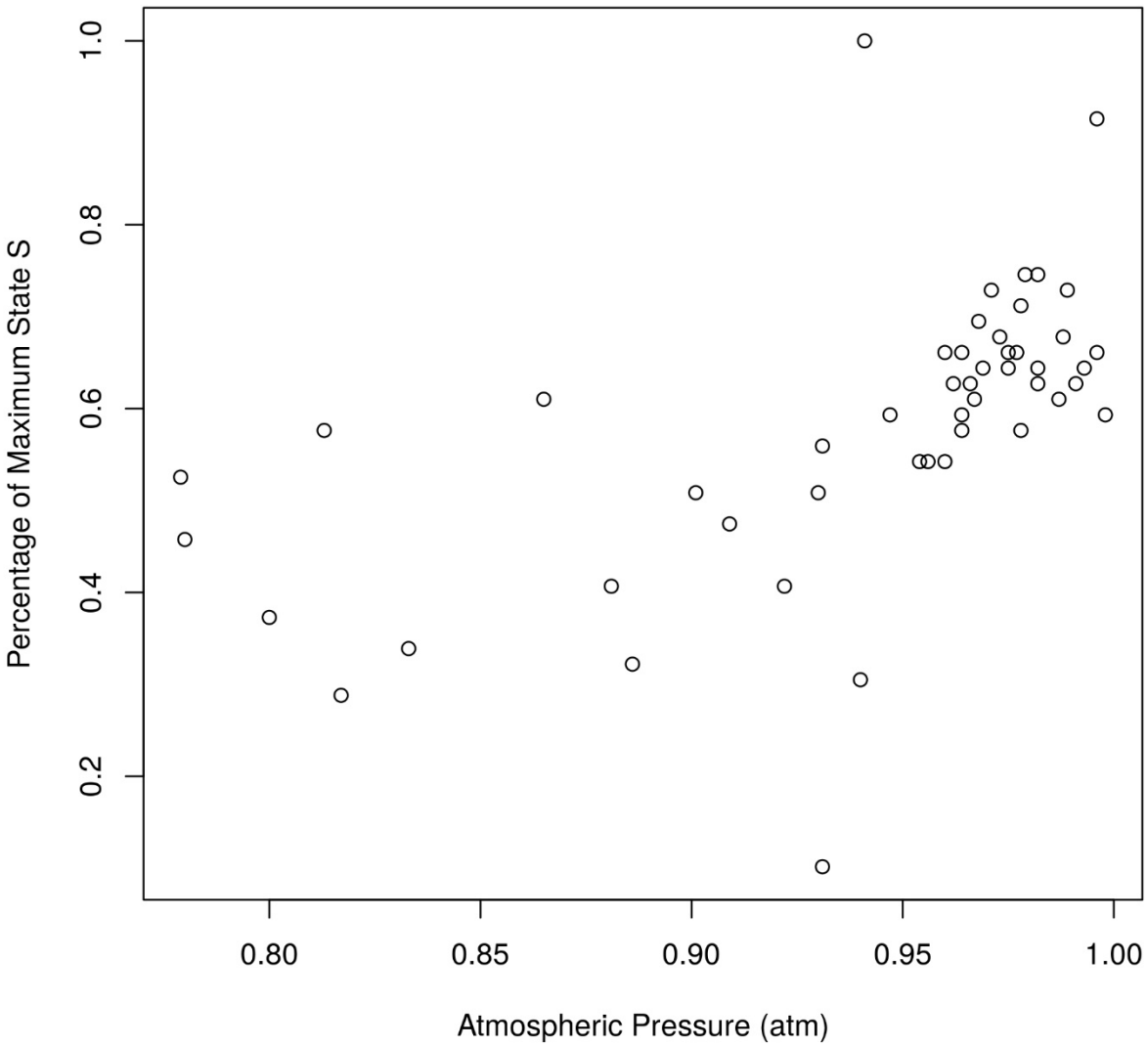
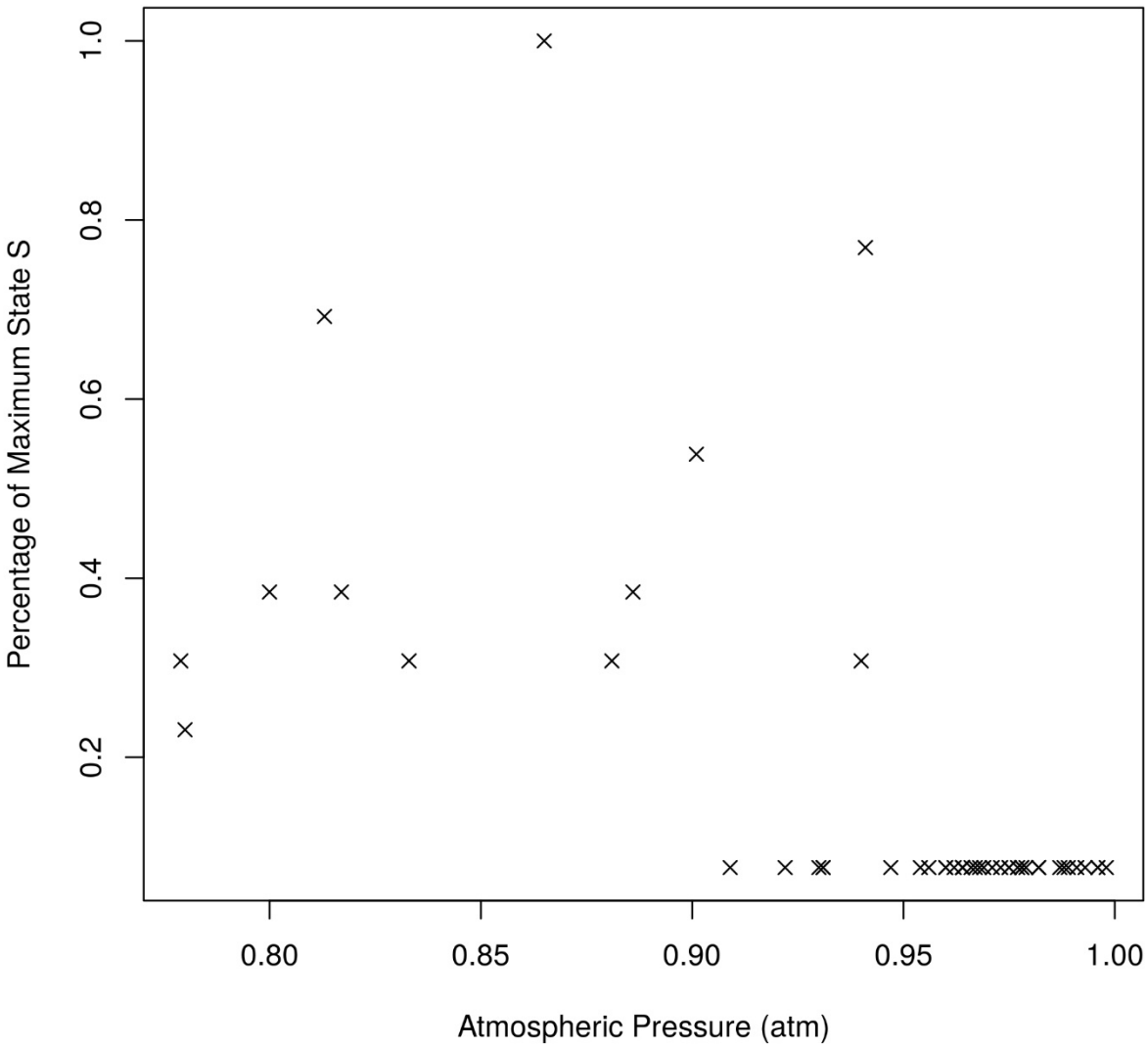

Percentage of Maximum State S
0.2
0.4
0.6
0.8
1.0
0.80
0.85
0.90
0.95
1.00
Atmospheric Pressure (atm)

Fig. 4b


Percentage of Maximum State S
0.2
0.4
0.6
0.8
1.0
0.80
0.85
0.90
0.95
1.00
Atmospheric Pressure (atm)