Rock-dwelling Spiny Lizards Take Advantage of Human-disturbed Habitat in the Trans-Mexican Volcanic Belt

by

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ABSTRACT

Human land use and land cover change alter key features of the landscape that may favor habitat selection by some species. Lizards are especially sensitive to these alterations because they rely on their external environment for regulating their body temperature. However, because of their diverse life-history traits and strategies, some are able to respond well to disturbance by using their habitat in various ways. To understand how they use their habitat and how human modifications may impact their ability to do this, biologists must identify where they occur and the habitat characteristics on which they depend. Therefore, I used species occupancy modeling to determine (1) whether disturbance predicts the presence of two sympatric congeneric (species of the same genus) lizard species *Sceloporus grammicus* and *S. torquatus*, and (2) which habitat characteristics are essential for predicting their occupancy and detection. I focused my study in central Mexico, a region of prevalent land use and land cover change. Here, I conducted visual encounter and habitat surveys at 100 1-hectare sites during the spring of 2019. I measured vegetation and ground cover, average tree diameter, and abundance of refuges. I recorded air temperature, relative humidity, and elevation. I summarized sites as either undisturbed or disturbed, based on the presence of human development. I also summarized sites by ecosystem type, desert or forest, based on vegetation composition (i.e., desert-adapted vs. non-desert-adapted plants), evidence of remnant forest, air temperature, and relative humidity. I found that *S. torquatus* was more likely to be present in disturbed habitat, whereas *S. grammicus* was more likely to be present in areas with leaf litter, tree cover, and woody debris. *S. torquatus* was twice as likely to be detected in forests than deserts, and *S. grammicus* was more likely to be detected at sites with high elevation and high relative humidity, low temperature, and herbaceous and grass cover. These results emphasize the utility of species occupancy modeling for estimating detection and occupancy in dynamic landscapes.

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INTRODUCTION

Overview and Purpose of Study

Human land use and land-cover change can alter key landscape features that many species depend on, such as heterogeneity, connectivity, vegetation structure, and vegetation composition (Aggemyr & Cousins, 2012; Malanson & Cramer, 1999; Pineda-Diez de Bonilla, León-Cortés, & Rangel-Salazar, 2012). The conversion of land for agriculture, mining, and urbanization is the primary contributor of land transformation and one of the leading causes of species decline and biodiversity loss worldwide (Chen et al., 2020; Johnson et al., 2020). Despite this, some taxa such as birds, reptiles, and mammals are able to persist in human-modified habitat (Cosentino, Schooley, Bestelmeyer, Campos, & Burkett, 2019; Kafley et al., 2019; Zurita & Bellocq, 2012). Their ability to exist in these areas may be attributed to various factors, such as the preference for habitat with varying physical features and climatic conditions, and the alteration of behavior and phenotype. For example, in urban regions, birds use artificial substrates as perches (e.g., roofs of buildings and homes, light posts), typically at high heights, for nesting, mating, and resting (Vogel, McCarron, & Zocche, 2018). Non-avian reptiles in these same regions also exploit artificial substrates for perching, at various heights and with many crevices, (e.g., pavers, brick or cement walls, and fences) to regulate their body temperature, seek refuge, or perform territorial and mating displays (Aviles-Rodriguez & Kolbe, 2019; C. L. Mensforth & C. Bull, 2008; Stroud et al., 2019). These taxa, and mammals, may also change their activity throughout the day to minimize encounters with predators and humans (Ladle, Steenweg, Shepherd, & Boyce, 2018;

Laursen, Møller, & Holm, 2016; Pizzatto, Child, & Shine, 2008). However, land use and land-cover change is likely to continue over the years, and some species may be unable to adapt rapidly. To help preserve these species, we must know which features facilitate their presence in these dynamic environments.

Lizards are vulnerable to land transformation because of their dependency on the external environment for regulating their body temperature (Khelifa et al. 2013; Pafilis et al. 2017). Mining, agriculture, livestock grazing, and urbanization create open, arid, high-temperature areas that are unsuitable for lizards and negatively affect their diversity compared to unmodified habitats (Berriozabal-Islas, Badillo-Saldana, Ramirez-Bautista, & Moreno, 2017; Glor, Flecker, Benard, & Power, 2001). However, because lizards are widespread and abundant compared to other non-avian reptiles and have various life-history strategies, some may respond well to different types of human disturbance (Aviles-Rodriguez & Kolbe, 2019; Battles, Moniz, & Kolbe, 2018; C. L. Mensforth & C. M. Bull, 2008; Smart, Whiting, & Twine, 2005; Webb & Shine, 2000). For example, in areas of low to moderate urban development, arboreal lizards are more common than terrestrial lizards because they readily climb building surfaces and exotic trees (Germaine & Wakeling, 2001). Arboreal lizards also fare better than terrestrial lizards in areas where livestock grazing significantly reduces complex ground structures because of their ability to exploit tree hollows (Neilly, Nordberg, VanDerWal, & Schwarzkopf, 2018). However, due to their dependency on trees, arboreal species may also be sensitive to high levels of disturbance (e.g., heavy forest clearing). In these situations, terrestrial lizards may be better off if artificial substrates, such as walls and fences, and refuges are abundant.

To understand how lizards use their habitat in diverse ways and how changes in habitat characteristics may impact their ability to do this, we must assess where individuals are present. However, their wariness and cryptic coloration added with landscape complexity (e.g., vegetation density and vertical structure) or inaccessible areas (e.g., steep slopes) that may create obstacles for observers, make their detectability low. Occasionally, this can lead to biased estimates of species presence due to misidentifications or false absences (Royle & Link, 2006). Species-occupancy modeling accounts for this imperfect detection by estimating the probabilities of both presence and detection by incorporating site-specific habitat and environmental covariates (Mackenzie et al., 2002; White & Cooch, 2018). These models have been widely used to assess the impact of disturbance, habitat heterogeneity, and environmental variables on the presence, co-occurrence, interactions, and habitat use of several taxa (e.g., felids, bats, and fish; Blanco & Garrie, 2020; Hubbell, Schaefer, Warren, & Sterling, 2020; Kafley et al., 2019; Paviolo et al., 2018). However, few studies have used these models for explaining associations between the presence and detection of sympatric congeneric (species of the same genus) lizard species and regions prevalent in land use and land-cover change.

In central Mexico, an estimated 550,000 hectares of forest and scrubland are cleared every year for different types of land use, namely cropland and urbanization (Mas et al., 2003). Although this rate has lowered over the years, deforestation continues (FAO, 2020). Consequently, the principal ecosystems that help support Mexico’s high lizard diversity may be at great risk of being altered even further. Owing to lizards’ heavy reliance on small areas within a large habitat (microhabitat, e.g., tree cavity) with specific climatic conditions (microclimate, e.g., rock crevice) for regulating their body temperature, they are particularly sensitive to the effects of habitat alteration and will likely be threatened as a consequence.

One of the most diverse lizard genera, *Sceloporus*, has the highest species diversity in central Mexico. These species are oviparous or viviparous and have a broad habitat selection. They occur in low-elevation deserts and high-elevation forests. Two species, *Sceloporus torquatus* and *S. grammicus* are closely related, and have wide, overlapping geographic ranges in central Mexico (Fig. 1; IUCN, 2020). Both are also dietary generalists, diurnal (active during the day), and females give birth to live young during the spring season. For *S. torquatus,* this season is in April or early May (Guillette & Méndez-de la Cruz, 1993), and for *S. grammicus*, in early spring (Jiménez-Cruz, Ramírez-Bautista, Marshall, Lizana-Avia, & de Oca, 2005). Both species also differ morphologically (IUCN, 2020). *S. torquatus* is a large species endemic to Mexico and widely distributed on the Central Plateau. It tends to occur in mountainous regions with rocky terrain, and in open coniferous and mixed forests at elevations 1000-3200 m (IUCN, 2020). Adult minimum snout-vent length at sexual maturity for both males and females is approximately 73 mm (Salgado Ugarte, 2001). Adult males are typically larger than females and have large blue and black ventral patches. Females also have colorful ventral patches but are smaller and less intense in coloration (Vargas-García, Argaez, Solano-Zavaleta, & Zúñiga-Vega, 2019). In contrast, *S. grammicus* is a small species found at low elevations in arid and semi-arid regions of southern Texas, and North and

Central Mexico at elevations up to 4600 m (Lemos-Espinal, Ballinger, & Smith, 1998a). It tends to occupy large mesquite trees, oaks, and other trees, such as nopales (*Opuntia ficus-indica*) (IUCN, 2020). Adult snout-vent length at sexual maturity for males is approximately 42.5 mm, and 40.7 mm for females (H. Pérez-Mendoza et al., 2014).

For this study, I used single-season, single-species occupancy models in tandem with principal component analysis to investigate the influence of habitat characteristics on the presence and detection of *Sceloporus torquatus* and *S. grammicus* in areas of land use and land-cover change. I incorporated environmental and climatic variables into my models, such as ground cover (Grimsley, Eamick, Carpenter, Ingraldi, & Leavitt, 2018), vegetation cover (Glavas et al., 2020; Pinto, Moreira, Freitas, & Santos, 2018), vertical vegetation structure (Castilla & Bauwens, 1992), air temperature, humidity (Dupoue et al., 2017; Huang, Kearley, Hung, & Porter, 2020), elevation (Escoriza, 2020), and the number of refuges (Howard & Hailey, 1999). I hypothesized that the influence of these variables on lizard presence will differ between these two species and that the larger, rock-dwelling species may be able to persist more in disturbed habitat compared to the smaller, arboreal species. More specifically, I asked (1) whether disturbance favors the presence of *Sceloporus grammicus* and *S. torquatus*, and (2) which habitat characteristics are essential for predicting the occupancy and detection of each species.

MATERIALS AND METHODS

Study Area

I conducted fieldwork in the spring of May 2019, a time of high viviparous lizard activity within the Trans-Mexican Volcanic Belt region of central Mexico. This region has undergone dramatic climate and geological change that has contributed to landscape heterogeneity, several volcanoes, and biodiversity (Mastretta-Yanes, Moreno-Letelier, Piñero, Jorgensen, & Emerson, 2015). Alpine grassland dominates at elevations greater than 3900 m, pine forest at elevations between 3500-3900 m, and pine-oak forest, shrubland, other grasslands, cropland, and desert at elevations lower than 3500 m (Mastretta-Yanes et al., 2015). This heterogeneous region allowed me to examine a variety of local-scale habitat features where two *Sceloporus* lizard species, *S. torquatus* and *S. grammicus*, occur. To incorporate variance in habitat characteristics and disturbance along different elevational gradients, I randomly selected 100, one-hectare, sampling sites across five Mexican states (Fig. 2). To ensure the independence of these study sites, I established them greater than 10 kilometers apart (H. A. Pérez-Mendoza et al., 2013). Varied land use (e.g., cropland, urbanization, and livestock grazing) occur at these sites.

Habitat and Visual Encounter Surveys

My field crew and I visited each site only once and during clement weather conditions (i.e., warm, sunny days, and wind from 0 to 3 on the Beaufort scale). First, at each site’s center point, I recorded the elevation (m), air temperature (°C), relative humidity (%), and wind speed (m/s). I also wrote a description of the site and its surroundings (e.g., type of vegetation, terrain, adjacent roads, and urban structures). If trees were present, I measured the diameter-at-breast-height for five trees, one located at each site's four boundaries and one closest to the site's center. Starting at the site's center, five observers and I walked in a random path within the one-hectare boundary and maintained a distance greater than or equal to five meters apart. At the same time, we visually surveyed the site for lizards for 15 minutes between 0800-1800 hrs. Each observer recorded the presence of all adult or subadult individuals. Observers also visually surveyed each site at various eye levels because *Sceloporus* lizards tend to select perches at different heights (Rummel & Roughgarden, 1985). Observers did not move any objects out of place nor communicate with each other about the lizards that they detected.

Following our visual encounter surveys, we conducted habitat surveys for each site for two minutes. At the end of each minute, each observer recorded the following habitat variables at a single point: vegetation cover, ground cover, leaf litter depth, leaf litter area, and the number of woody debris. We classified vegetation cover as either tree, shrub, or herbaceous plant. We classified ground cover as anything covering the bare soil surface, such as grass, gravel (0.2-25.6 cm), boulder (>25.6 cm), course (≥10 cm diam.) and fine (<10 cm) woody debris, and leaf litter (Dahlberg et al., 2011; Sprague, Bateman, & Somers, 2018; USDA, 2020; Wentworth, 1922). We recorded the bare soil surface as bare soil. Each observer recorded leaf litter depth (cm) and visually estimated leaf litter area (%) inside a 0.5 m by 0.5 m quadrat. Observers counted the number of times that woody debris intersected a meter stick laid on the ground surface. Following the completion of each survey, we scored the abundance of likely refuges using an ordinal scale, 0: no refuges present, 1: refuges rarely present, 2: refuges common, and 3: refuges abundant.

Disturbance and Ecosystem Classification

I summarized ecosystem type as desert or forest and based this decision on vegetation composition (i.e., trees, shrubs, herbaceous and desert-adapted plants), evidence of remnant forest, air temperature, and relative humidity. Sites with high air temperature, low relative humidity, and the presence of desert plants were considered desert; otherwise, they were considered a forest. I also categorized each site as undisturbed or disturbed, based on the level of human development (i.e., number of human-made trails/roads, urban structures, and agriculture). I placed sites with very few human-made trails, urban structures, adjacent roads, and with intact desert or forest, in the undisturbed category. I placed sites that did not meet this criterion in the disturbed category.

Data Analysis

For my statistical analysis, I averaged all twelve sample points (2 sample points per observer) per site for percent vegetation and ground cover, leaf litter depth, leaf litter area, and woody debris count. I standardized raw continuous variables using the R statistical programming standardize function (R package “effectsize”, version 0.3.0; R Core Team, 2018). I ran a Principal Component Analysis in R using the principal function (R package “psych”, version 1.9.12.31; R Core Team, 2018) to reduce 17 habitat variables to fewer, uncorrelated components. I excluded binary data (i.e., ecosystem and disturbance) from my principal component analysis. I applied a varimax rotation for this analysis to retain components with high variance and to simplify interpretation of my results. I retained only principal components that explained more than 9% variance (Legendre & Legendre, 2012). I interpreted these components based on variables with loadings greater than 0.5 (Legendre & Legendre, 2012). I then used these principal component scores as predictor variables in single-species, single-season occupancy models using MARK program (Mackenzie et al., 2002; White & Cooch, 2018) to estimate the probability of detection and occupancy for *S. torquatus* and *S. grammicus*. I fit 195 models for each species, with additive combinations of principal components, ecosystem, and disturbance as predictor variables. I also implemented models in which neither detection nor occupancy were affected by these variables. For the response variable, I used an encounter history, a sequence of zeroes and ones, “0”, indicating a species was not detected or “1”, indicating a species was detected at each site. I then compared models using the Akaike Information Criterion (AIC) (Akaike, 1987). I compared AIC values for each model with the AIC for the null model to determine the level of empirical support.

RESULTS

Principal Component Analysis

My principal component analysis reduced 17 habitat variables to six principal components with eigenvalues greater than one. However, I used only the first four principal components for my models and based this decision on how much cumulative explained variance was gained by retaining additional components, less than 9% (Table 1). I interpreted these four principal components as follows: PC1: wooded, PC2: open, herbaceous, grassy, PC3: microclimate (high humidity and low temperature), and PC4: shrubs and small trees.

Species Occupancy Modeling

A comparison of the null model with the model that incorporated disturbance as a covariate of occupancy showed that we found *S. torquatus* lizards more often in disturbed than in undisturbed sites (Fig. 3; Table 2, 4). Conversely, disturbance did not significantly predict *S. grammicus* occupancy (Table 3, 5). Also, I found that different habitat variables predicted the occupancy and detection of the two lizard species (Fig. 3-4, Table 2-3). For *S. torquatus,* the best-supported model incorporated disturbance as a predictor for occupancy and forested ecosystem as a predictor for detection. *S. torquatus* was approximately three and a half times more likely to be present in disturbed (occupancy = 0.51) than undisturbed habitat (occupancy = 0.14) and twice as likely to be detected in forests (detection = 0.42) than in deserts (detection = 0.21). This model ranked higher than all other models, including the null. The next best-supported model emphasized the importance of ecosystem type, wooded component, and microclimate component in determining *S. torquatus* detection (Table 2). We detected *S. torquatus* over three times more often in forests (detection = 0.44) than in deserts (detection = 0.13), and detection of this species was negatively associated with the wooded component, but positively associated with the microclimate component.

The best-supported model results for *S. grammicus* showed that the additive effect of the wooded component and the shrub cover, small tree component, were significant predictors for occupancy. This model also showed that the additive effect of the open, herbaceous, grassy component, and microclimate component, were important predictors for detection. The wooded component was positively associated with occupancy, and the shrub, small tree component was negatively associated; however, the effect was not statistically different from zero. This indicates that *S. grammicus* is more likely to be present in habitat with plenty of leaf litter, tree cover, woody debris, and scarce grass cover. The additive effect of the open, grassy, herbaceous, grassy component, and microclimate component were positively associated with detection. This indicates that *S. grammicus* is more likely to be detected in open habitat, at high elevation, with an abundance of grass and herbaceous cover, and little bare soil. It also indicates that this species is more likely to be detected at sites with high relative humidity, low temperatures, and abundant gravel cover. This model ranked higher than all other models, including the null.

DISCUSSION AND CONCLUSION

Summary of Findings

Overall my results showed that disturbance affected the presence and detection of *S. torquatus* and *S. grammicus* differently. The best-supported model results showed that *S. torquatus* was more likely to be present in disturbed habitat, whereas *S. grammicus* was not. In contrast, *S. grammicus* was more likely to be present in areas with an abundance of leaf litter cover, tree cover, woody debris, and scarce grass cover. For detection, *S. torquatus* was twice as likely to be detected in forests than deserts and had a high probability of being detected at sites with high humidity and low temperature. Conversely, *S. grammicus* had a high likelihood of being detected at locations with an abundance of herbaceous and grass cover, scarce bare soil, high elevation, high relative humidity, and low temperature.

Effects of Disturbance and Habitat Variables on Occupancy

The much higher probability of predicting *S. torquatus* presence in disturbed habitat compared to *S. grammicus* may suggest that rock-dwelling lizard species are more tolerant of disturbance than arboreal lizard species. A terrestrial lizard species, *Tropidurus hispidus*, persists more in urban than natural environments, perhaps because it makes use of artificial substrates such as cement walls and construction materials that may resemble rocky outcrop habitat in which it evolved (Andrade, 2020). Similarly, *S. torquatus* may exploit artificial substrates in disturbed areas to respond to conditions that somewhat resemble those in which it tends to occur, open rocky and forested habitat (IUCN, 2020). Also, artificial structures may share similar physical and thermal properties as rocks that offer suitable areas for rock-dwelling reptile species to bask and seek refuge (C. L. Mensforth & C. Bull, 2008; Webb & Shine, 2000).

Unlike *S. torquatus*, tree cover, leaf litter, and woody debris were more important for *S. grammicus* presence. This finding suggests that arboreal lizards may not fare well in disturbed habitat because they tend to use trees, which typically are low in abundance in these areas (Alcala, Alcala, & Dolino, 2004). Additionally, because *S. grammicus* lizards are more cryptic in coloration than are *S. torquatus* lizards, they may avoid human-modified habitat and select intact forests where they can blend in with the natural background and evade predators. Similarly, moths (*Hypomecis roboraria* and *Jankowskia fuscaria*), desert tortoises (*Gopherus agassizii*), and chameleons (*Furcifer viridis*), prefer habitats and backgrounds that make them inconspicuous to predators (Kang, Stevens, Moon, Lee, & Jablonski, 2015; Nafus et al., 2015; Resetarits & Raxworthy, 2016).

Differences in body size between *S. grammicus* and *S. torquatus* lizards may also explain the ability of one species to persist well in disturbed habitats. *S. torquatus* lizards are much larger in body size compared to *S. grammicus* lizards, and larger animals may be better able to persist in disturbed habitats. This finding may be consistent with evidence from a previous study that found that *Anolis sagrei* lizards in disturbed habitat were significantly larger in snout-vent length than those in natural habitat, even though the two populations were not genetically distinct from each other (Marnocha, Pollinger, & Smith, 2011). Additional research is needed into the possibility of character displacement and other interspecific effects.

Effects of Disturbance and Habitat Variables on Detection

Disturbance was not an important predictor of detection for either species. Instead, *S. torquatus* was more likely to be detected in forests than deserts, and at sites with low temperature, high humidity, low tree cover, little woody debris, and little leaf litter. *S. torquatus* tends to occur mostly at high elevations in mountainous regions with open coniferous and mixed forests (IUCN, 2020). These high elevation forests are typically lower in temperature and higher in humidity compared to deserts at lower elevations. High humidity conditions are associated with high richness and abundance in forest-dwelling reptiles (Cabrera-Guzmán & Reynoso, 2012). We need additional studies to explore the importance of humidity also in detection.

In comparison with *S. torquatus*, *S. grammicus* was more likely to be detected at sites with low temperatures, high humidity, high elevation, an abundance of herbaceous plants, grass, gravel, and scarce bare soil. Its diverse habitat use may also explain why it is easier to detect at sites with abundant herbaceous cover, grass, and gravel cover (Leyte-Manrique, Hernández-Salinas, Ramírez-Bautista, Mata-Silva, & Marshall, 2017). Also, it may be easier to detect at sites with these habitat characteristics because its coloration or patterning contrasts with its natural background (Orton, McElroy, & McBrayer, 2018). However, a tradeoff may exist wherein the benefit of food opportunities may be greater than the cost of being conspicuous to predators, thereby enabling it to occur in these areas, especially if refuges are in abundance (Drakeley, Lapiedra, & Kolbe, 2015). Finally, forest clearing for different types of land use, such as cropland, pasture, and urban development, contributes to landscape fragmentation and creates open areas that could increase the detectability of this species (Dixo & Metzger, 2009).

Implications

Given that Mexico is a developing country, with a population growth of +10% by the year 2100, and ranked number two among U.S. agricultural export markets (United Nations & DESA, 2019; USDA, 2020), what will the fate of Mexico's high reptilian diversity be? Future projections predict that if Mexico continues with medium population and economic growth, rates of land use, land-cover change, and climate change, severe loss of forests for rainfed and irrigated agriculture will occur by the year 2100(Mendoza-Ponce, Corona-Núñez, Kraxner, Leduc, & Patrizio, 2018). Consequently, reptilian diversity may be at an increased risk of threat. Therefore, enhancing our understanding of features of the landscape that enable reptilian persistence, and directing conservation efforts towards maintaining these features, is critical for ensuring their vitality in the continual presence of environmental change. This is especially crucial for inconspicuous and wary reptiles that often are misidentified or incorrectly marked absent in the field and may lead to inaccurate estimates of their presence and detection. Thus, the integration of principal component analysis and species occupancy modeling may be instrumental for implementing these conservation efforts because it can inform scientists about where reptiles are more likely to occur and be detected. Doing so could ensure that appropriate actions be taken to better conserve their habitat in areas of land use and land-cover change.

Table 1. Rotated principal component loadings for 17 habitat variables. High loadings (>0.5) are highlighted in gray. Negative and positive values indicate inverse

Habitat Variable	PC1	PC2	PC3	PC4
leaf litter area	0.95	0.09	-0.11	-0.13
leaf litter	0.93	0.11	-0.17	-0.16
leaf litter depth	0.88	0.11	-0.17	-0.15
tree	0.75	-0.10	0.07	0.05
woody debris count	0.73	-0.11	0.28	0.18
grass	-0.52	0.75	-0.01	0.06
herbaceous	-0.26	0.81	0	0.02
bare soil	-0.39	-0.70	-0.09	0.15
elevation	0.07	0.54	-0.06	-0.22
relative humidity	-0.10	0.17	0.79	0.01
air temperature	-0.21	-0.25	-0.67	0.37
shrub	0.13	0.06	0.03	0.82
average tree diameter-at-breast-height	0.33	0.11	0.07	-0.63
fine wood	0.30	-0.18	0.35	0.19
boulder	-0.19	-0.45	0.13	-0.29
gravel	-0.10	-0.22	0.51	0.01
refuges	-0.08	-0.19	0.34	0.32
Proportion Variance Explained (%)	26	15	10	9
Cumulative Variance Explained (%)	26	41	51	61

Table 2. Top 10 model results for *S. torquatus* detection (p) and occupancy (ψ) with ΔAIC < 7, plus null model (see Table 4 for full result summary)

Model	df	AIC	ΔAIC	Weight	β(SE)	95% CI
p(ecosystem), ψ(disturbance)	4	383.3	0	0.17	forest: -0.3(0.20) desert: -1.3(0.31) disturbed: 0.1(0.32) undisturbed: -1.8(0.64)	-0.70, 0.10 -1.95, -0.73 -0.58, 0.69 -3.06, -0.56
p(ecosystem + PC1 + PC3), ψ(constant)	5	385.1	1.80	0.06	p_{int}: -1.9(0.36) ecosystem: 1.6(0.41) PC1: -0.6(0.22) PC3: 0.4(0.21) ψ_{int}: -0.1(0.34)	-2.58, -1.18 0.81, 2.43 -1.03, -0.18 0.03, 0.84 -0.71, 0.60
p(constant), ψ(disturbance + PC4)	4	385.8	2.51	0.05	p_{int}: -0.7(0.17) ψ_{int}: -0.2(0.27) disturbance: 1.6(0.69) PC4: -0.6(0.28)	-0.98, -0.33 -0.79, 0.28 -2.96, -0.26 -1.17, -0.08
p(constant), ψ(disturbance + PC3 + PC4)	5	386.1	2.86	0.04	p_{int}: -0.7(0.17) ψ_{int}: -0.2(0.28) disturbance: -1.7(0.70) PC3: 0.3(0.27) PC4: -0.6(0.29)	-1.74, -0.62 0.17, 1.54 -0.98, 0.04 -1.14, -0.10
p(ecosystem), ψ(PC4)	4	386.2	2.93	0.04	p_{int}: -1.2(0.29) ecosystem: 0.9(0.35) ψ_{int}: -0.5(0.26) PC4: -0.6(0.26)	-0.99, -0.33 -0.77, 0.32 -3.08, -0.34 -0.19, 0.86 -1.19, -0.07
p(constant), ψ(ecosystem + disturbance)	4	386.7	3.35	0.03	p_{int}: -0.6(0.16) ψ_{int}: -0.6(0.33) ecosystem: 1.1(0.49) disturbance: -1.7(0.69)	-0.97, -0.32 -1.26, 0.02 0.12, 2.05 -3.04, -0.36
p(ecosystem), ψ(PC3 + PC4)	5	386.9	3.66	0.02	p_{int}: -1.2(0.29) ecosystem: 0.9(0.36) ψ_{int}: -0.5(0.27) PC3: 0.3(0.27) PC4: -0.6(0.27)	-1.79, -0.64 0.19, 1.59 -0.99, 0.07 -0.24, 0.84 -1.18, -0.10
p(ecosystem), ψ(PC1 + PC4)	5	387.1	3.77	0.02	p_{int}: -1.3(0.31)	-1.86, -0.65 0.22, 1.66

					ecosystem: 0.9(0.37) ψ_{int}: -0.4(0.28) PC1: -0.3(0.25) PC4: -0.6(0.27)	-0.98, 0.12 -0.76, 0.23 -1.16, -0.10
p(PC1), ψ(ecosystem + disturbance)	5	387.3	4.01	0.02	PC1: -0.3(0.23) p_{int}: -0.7(0.17) ψ_{int}: -0.6(0.33) ecosystem: 1.2(0.54) disturbance: -1.6(0.71)	-2.34, -0.95 0.59, 2.19 -0.97, -0.10 -0.81, 0.41
p(ecosystem + PC1), ψ(constant)	4	387.4	4.07	0.02	p_{int}: -1.6(0.35) ecosystem: 1.4(0.41) PC1: -0.5(0.22) ψ_{int}: -0.2(0.31)	-0.71, 0.17 -1.03, -0.36 -1.28, 0.00 0.18, 2.32 -3.01, -0.25
null	2	396.7	13.38	0	p_{int}: -0.6(0.17) ψ_{int}: -0.5(0.23)	-0.98, -0.33 -0.98, -0.09

Table 3. Top 10 model results for *S. grammicus* detection (p) and occupancy (ψ) with ΔAIC < 7, plus null model. (see Table 5 for full result summary)

Model	df	AIC	ΔAIC	Weight	β(SE)	95% CI
p(PC2 + PC3), ψ(PC1 + PC4)	6	285.6	0	0.25	PC2: 0.7(0.21)	0.30, 1.13
					PC3: 0.8(0.29)	0.28, 1.41
					p_{int}: -1.1(0.22)	-1.55, -0.70
					ψ_{int}: -0.8(0.30)	-1.35, -0.19
					PC1: 0.6(0.32)	0.01, 1.26
					PC4: -0.5(0.29)	-1.05, 0.08
p(PC2 + PC3), ψ(PC1)	5	286.6	1.00	0.18	PC2: 0.7(0.21)	0.32, 1.15
					PC3: 0.8(0.29)	0.29, 1.41
					p_{int}: -1.1(0.22)	-1.56, -0.71
					ψ_{int}: -0.7(0.29)	-1.29, -0.15
					PC1: 0.6(0.30)	0.02, 1.19
p(PC2 + PC3 + PC4), ψ(PC1)	6	288.1	2.48	0.07	PC2: 0.7(0.21)	0.33, 1.14
					PC3: 0.8(0.29)	0.29, 1.41
					PC4: -0.2(0.29)	-0.77, 0.36
					p_{int}: -1.2(0.23)	-1.65, -0.74
					ψ_{int}: -0.7(0.29)	-1.26, -0.12
					PC1: 0.6(0.30)	0.01, 1.18
p(PC2 + PC3), ψ(PC4)	5	288.9	3.23	0.06	PC2: 0.7(0.21)	0.32, 1.14
					PC3: 0.8(0.29)	0.23, 1.35
					p_{int}: -1.1(0.21)	-1.52, -0.68
					ψ_{int}: -0.7(0.28)	-1.30, -0.21
					PC4: -0.4(0.27)	-0.97, 0.09
p(PC2 + PC3), ψ(ecosystem)	5	288.9	3.23	0.06	PC2: 0.7(0.21)	0.30, 1.13
					PC3: 0.8(0.29)	0.26, 1.38
					p_{int}: -1.1(0.22)	-1.53, -0.68
					ψ_{int}: -1.1(0.36)	-1.76, -0.36
					ecosystem: 0.8(0.53)	-0.16, 1.90
p(disturbance + PC2 + PC3), ψ(constant)	5	289.0	3.39	0.05	p_{int}: -1.0(0.23)	-1.42, -0.53
					disturbance: -0.8(0.53)	-1.86, 0.20
					PC2: 0.8(0.21)	0.37, 1.20
					PC3: 0.9(0.29)	0.30, 1.43
					ψ_{int}: -0.6(0.28)	-1.19, -0.11
p(PC2 + PC3), ψ(constant)	4	289.6	4.02	0.04	PC2: 0.7(0.21)	0.33, 1.15
					PC3: 0.8(0.28)	0.26, 1.37
					p_{int}: -1.1(0.22)	-1.53, -0.69
					ψ_{int}: -0.7(0.27)	-1.23, -0.16
p(ecosystem + PC2 + PC3), ψ(constant)	5	290.2	4.53	0.03	p_{int}: -1.4(0.36)	-2.16, -0.75
					ecosystem: 0.6(0.46)	-0.33, 1.46
					PC2: 0.6(0.22)	0.22, 1.07
					PC3: 0.9(0.30)	0.35, 1.51
					ψ_{int}: -0.6(0.28)	-1.18, -0.08

p(PC2 + PC3), ψ(ecosystem + disturbance)	6	290.3	4.71	0.02	PC2: 0.7(0.21) PC3: 0.8(0.28) p_{int}: -1.1(0.22) ψ_{int}: -0.9(0.40) ecosystem: 0.8(0.53) disturbance: -0.4(0.62)	0.30, 1.13 0.27, 1.39 -1.53, -0.69 -1.71, -0.16 -0.21, 1.87 -1.65, 0.77
p(PC2 + PC3 + PC4), ψ(ecosystem)	6	290.6	4.95	0.02	PC2: 0.7(0.21) PC3: 0.8(0.28) PC4: -0.2(0.30) p_{int}: -1.2(0.24) ψ_{int}: -1.0(0.37) ecosystem: 0.8(0.53)	0.31, 1.13 0.27, 1.39 -0.75, 0.43 -1.62, -0.70 -1.74, -0.30 -0.22, 1.88
null	5	301.9	16.27	0.02	p_{int}: -0.9(0.21) ψ_{int}: -0.9(0.25)	-1.30, -0.48 -1.41, -0.42

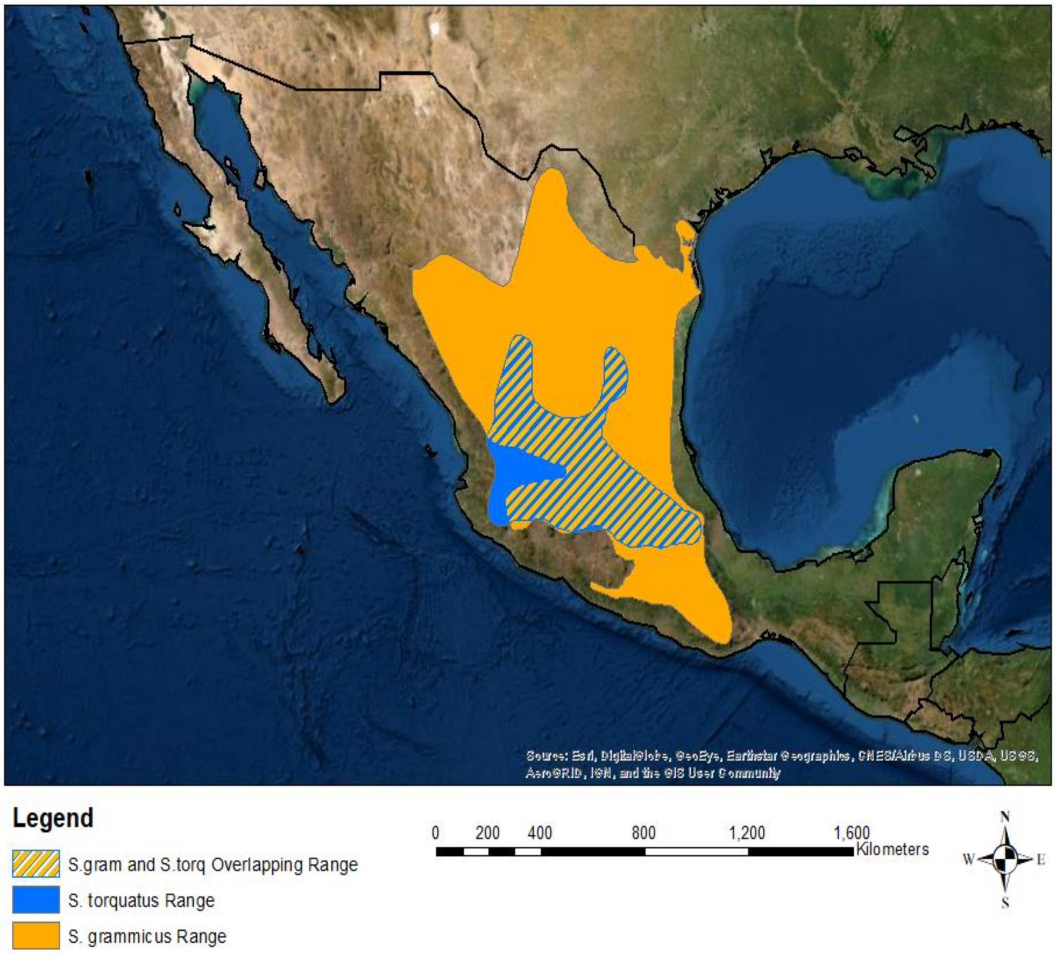

Figure 1. Map of Mexico showing *S. torquatus* and *S. grammicus* geographic range and range overlap

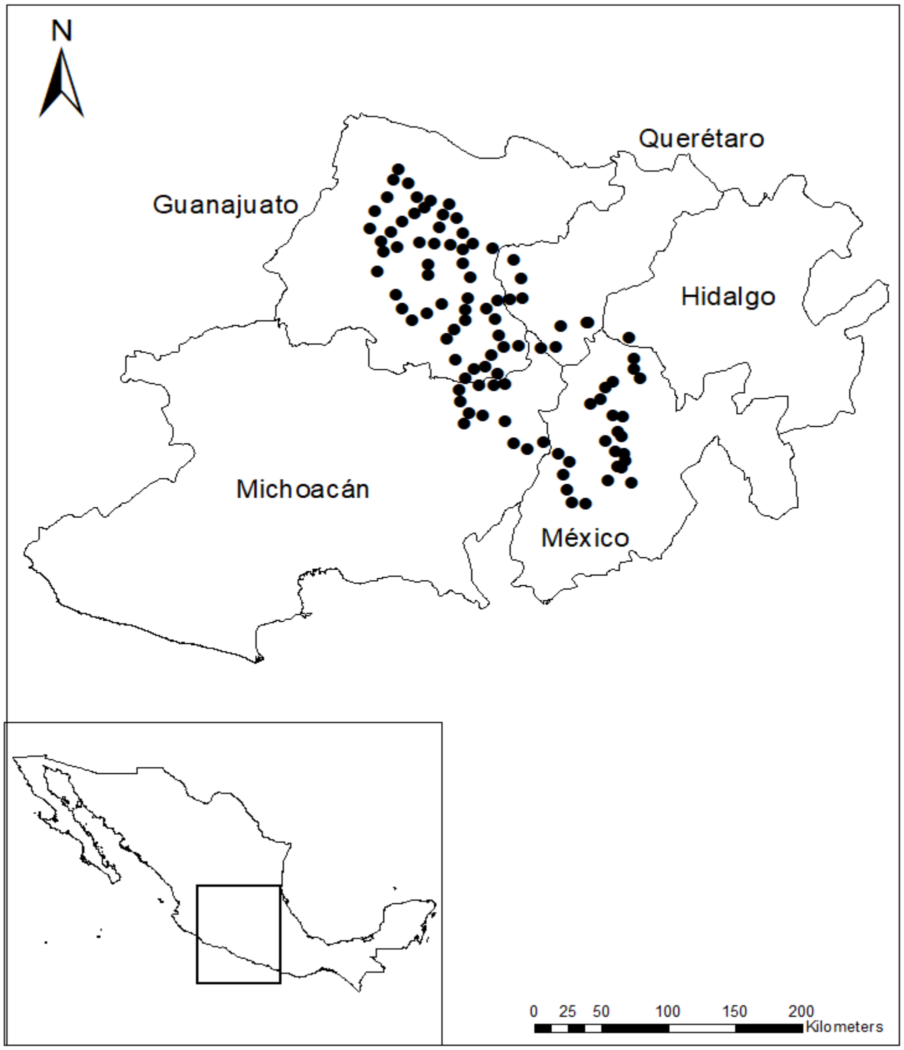

Figure 2. Map showing study area and 100 randomly selected field sites across five Mexican states

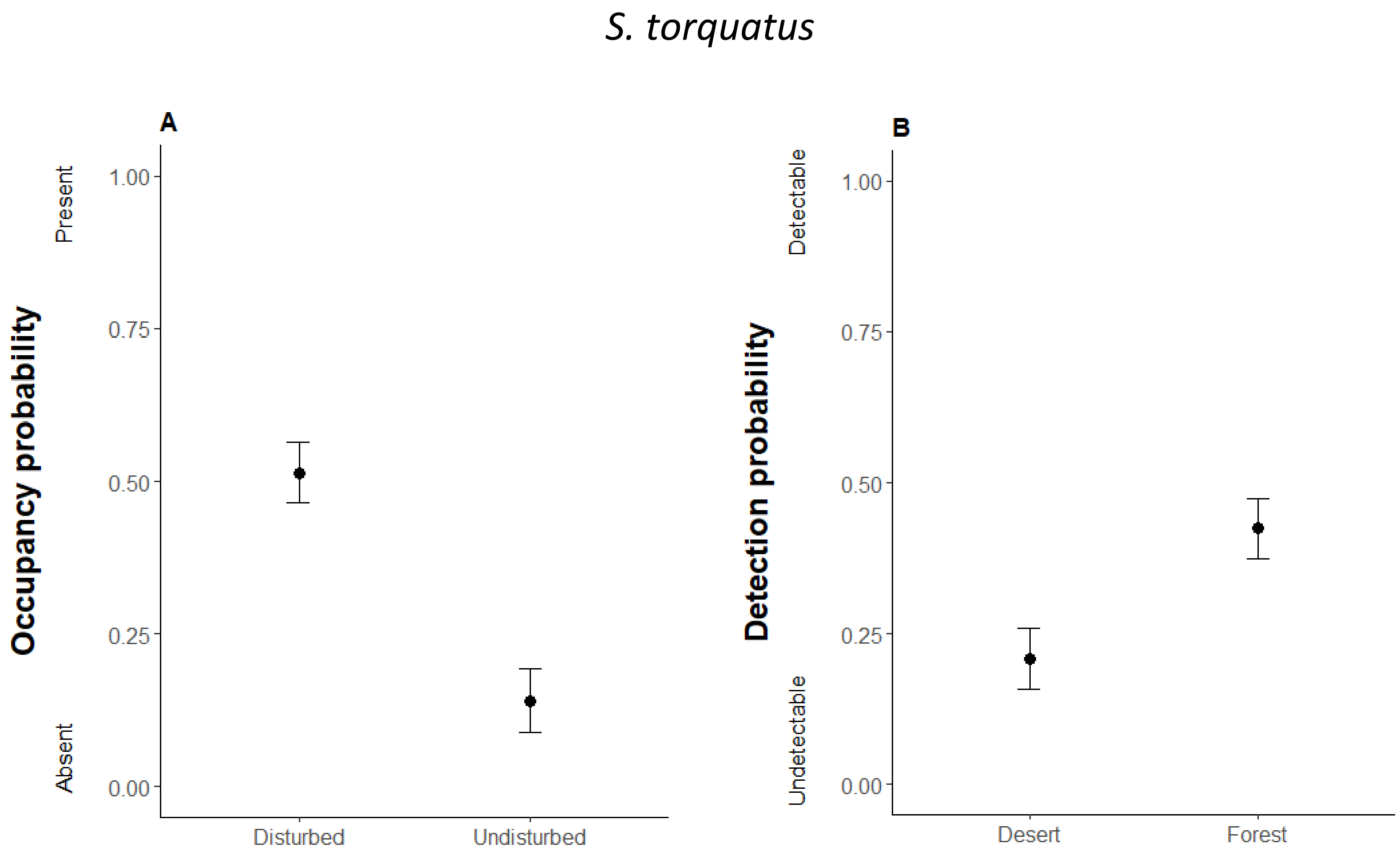

Figure 3. Best-fit model results for *S. torquatus* showing **(A)** occupancy vs. level of disturbance, and **(B)** detection vs. ecosystem type. Bars represent standard errors.

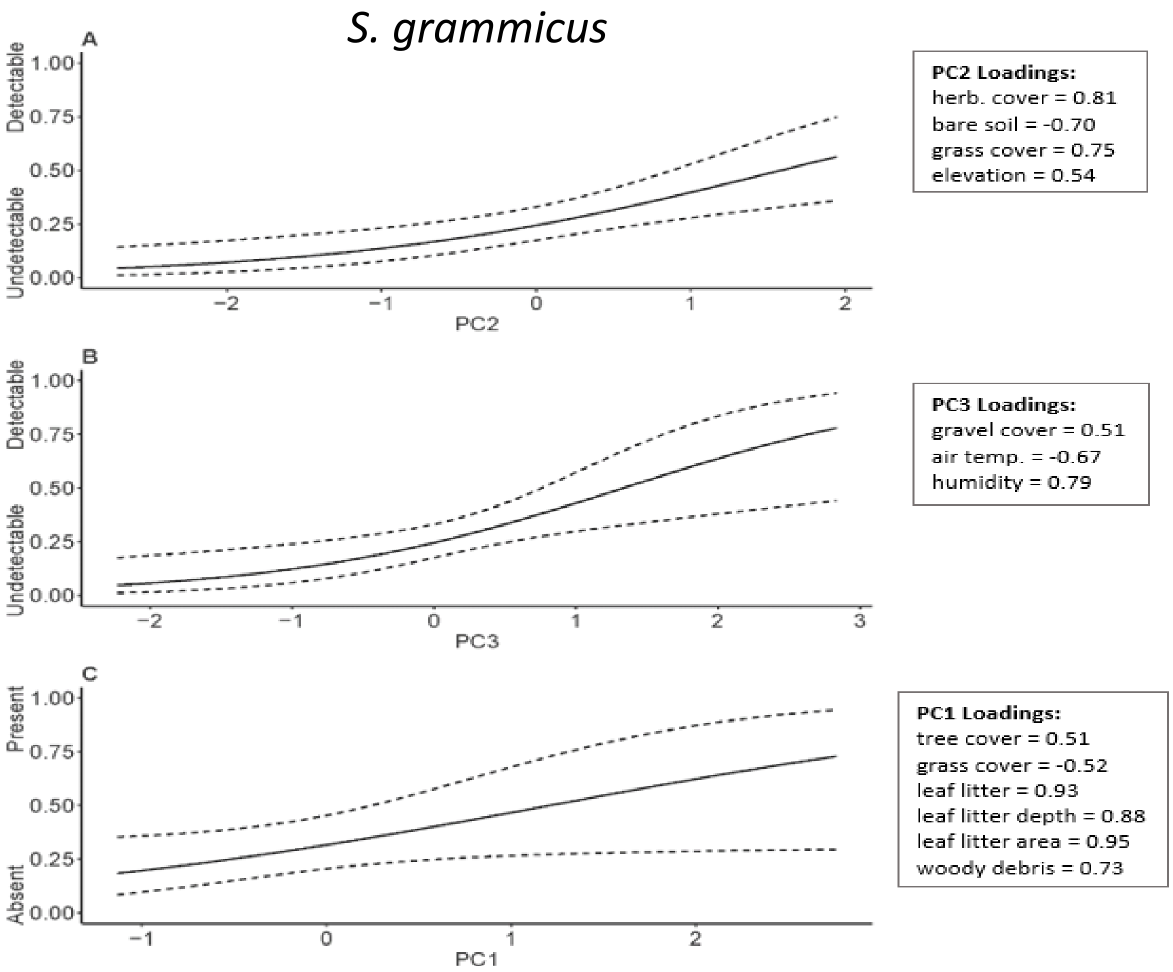

Figure 4. Best-fit model results, in standardized form, for *S. grammicus*: **(A, B)** detection vs. PC2 + PC3, **(C)** occupancy vs. PC1. Solid line indicates occupancy or detection estimate and broken line indicates 95% CI.

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APPENDIX A

FULL RESULTS FOR *S. TORQUATUS* DETECTION AND OCCUPANCY

Table 4. List of Models Run for *S. torquatus,* (p = detection, ψ = occupancy)

Model	df	AICc	ΔAICc	Weight
p(ecosystem), ψ(disturbance)	4	383.7	0	0.17
p(ecosystem + PC1 + PC3), ψ(constant)	5	385.7	2.0	0.06
p(constant), ψ(disturbance + PC4)	4	386.2	2.5	0.05
p(ecosystem), ψ(PC4)	4	386.7	2.9	0.04
p(constant), ψ(disturbance + PC3 + PC4)	5	386.8	3.1	0.04
p(constant), ψ(ecosystem + disturbance)	4	387.1	3.3	0.03
p(ecosystem), ψ(PC3 + PC4)	5	387.6	3.9	0.02
p(ecosystem), ψ(PC1 + PC4)	5	387.7	4.0	0.02
p(ecosystem + PC1), ψ(constant)	4	387.8	4.1	0.02
p(PC1), ψ(ecosystem + disturbance)	5	388.1	4.2	0.02
p(ecosystem + disturbance), ψ(PC4)	5	388.1	4.2	0.02
p(constant), ψ(disturbance + PC2 + PC4)	5	388.1	4.4	0.02
p(PC3), ψ(ecosystem + disturbance)	5	388.1	4.4	0.02
p(constant), ψ(disturbance + PC1 + PC4)	5	388.4	4.7	0.02
p(ecosystem), ψ(PC1 + PC3 + PC4)	6	388.7	4.9	0.01
p(ecosystem), ψ(PC2 + PC4)	5	388.7	4.9	0.01
p(PC1 + PC3), ψ(ecosystem + disturbance)	6	388.7	5.0	0.01
p(ecosystem + disturbance), ψ(PC3 + PC4)	6	388.8	5.1	0.01
p(constant), ψ(ecosystem + PC1 + PC4)	5	388.9	5.2	0.01
p(ecosystem + PC1 + PC2), ψ(constant)	5	388.9	5.2	0.01
p(constant), ψ(ecosystem + PC1 + PC3)	5	389.1	5.3	0.01
p(PC4), ψ(ecosystem + disturbance)	5	389.1	5.4	0.01
p(constant), ψ(ecosystem + PC1)	4	389.2	5.5	0.01
p(PC2), ψ(ecosystem + disturbance)	5	389.3	5.5	0.01
p(ecosystem + disturbance), ψ(PC1 + PC4)	6	389.3	5.6	0.01
p(ecosystem + PC1 + PC4), ψ(constant)	5	389.5	5.8	0.01
p(ecosystems), ψ(ecosystems)	4	389.6	5.9	0.01
p(disturbance), ψ(PC4)	4	389.6	5.9	0.01
p(ecosystem), ψ(PC2 + PC3 + PC4)	6	389.7	5.9	0.01
p(ecosystem), ψ(PC1 + PC2 + PC4)	6	389.8	6.1	0.01
p(constant), ψ(disturbance)	3	389.9	6.2	0.01
p(ecosystem + disturbance), ψ(PC2 + PC4)	6	390.1	6.3	0.01
p(PC1 + PC2), ψ(ecosystem + disturbance)	6	390.1	6.4	0.01
p(PC1 + PC4), ψ(ecosystem + disturbance)	6	390.1	6.4	0.01
p(PC3 + PC4), ψ(ecosystem + disturbance)	6	390.2	6.4	0.01
p(ecosystem + PC3), ψ(constant)	4	390.2	6.5	0.01
p(constant), ψ(disturbance + PC3)	4	390.3	6.5	0.01
p(disturbance), ψ(ecosystem)	4	390.3	6.6	0.01

p(PC2 + PC3), ψ(ecosystem + disturbance)	6	390.4	6.6	0.01
p(constant), ψ(ecosystem + PC4)	4	390.4	6.7	0.01
p(ecosystem), ψ(constant)	3	390.7	6.9	0.01
p(constant), ψ(PC4)	3	390.8	7.0	0.01
p(disturbance), ψ(PC3 + PC4)	5	390.8	7.1	0.01
p(ecosystem), ψ(PC1 + PC2 + PC3 + PC4)	7	390.8	7.1	0.00
p(constant), ψ(ecosystem + PC1 + PC2)	5	391.1	7.4	0.00
p(ecosystem + PC2 + PC3), ψ(constant)	5	391.1	7.4	0.00
p(PC3), ψ(disturbance)	4	391.1	7.4	0.00
p(constant), ψ(ecosystem + PC3 + PC4)	5	391.1	7.4	0.00
p(ecosystem + disturbance), ψ(constant)	4	391.3	7.6	0.00
p(PC2 + PC4), ψ(ecosystem + disturbance)	6	391.3	7.6	0.00
p(ecosystem), ψ(PC1)	4	391.4	7.7	0.00
p(disturbance), ψ(PC2 + PC4)	5	391.5	7.7	0.00
p(PC4), ψ(disturbance)	4	391.5	7.8	0.00
p(ecosystem), ψ(PC3)	4	391.6	7.8	0.00
p(PC1), ψ(disturbance)	4	391.7	7.9	0.00
p(disturbance), ψ(PC1 + PC4)	5	391.8	8.0	0.00
p(ecosystem + disturbance), ψ(PC3)	5	391.8	8.1	0.00
p(PC1), ψ(ecosystem)	4	391.8	8.1	0.00
p(constant), ψ(disturbance + PC2)	4	391.8	8.1	0.00
p(ecosystem + PC2), ψ(constant)	4	391.8	8.1	0.00
p(ecosystem + PC3 + PC4), ψ(constant)	5	391.9	8.2	0.00
p(disturbance), ψ(disturbance)	4	391.9	8.2	0.00
p(constant), ψ(PC3 + PC4)	4	392.0	8.3	0.00
p(PC2), ψ(disturbance)	4	392.0	8.3	0.00
p(constant), ψ(disturbance + PC1)	4	392.1	8.4	0.00
p(ecosystem + PC4), ψ(constant)	4	392.2	8.4	0.00
p(constant), ψ(disturbance + PC2 + PC3)	5	392.2	8.4	0.00
p(ecosystem + disturbance), ψ(PC1)	5	392.3	8.6	0.00
p(ecosystem), ψ(PC1 + PC3)	5	392.4	8.6	0.00
p(constant), ψ(disturbance + PC1 + PC3)	5	392.4	8.7	0.00
p(PC1 + PC3), ψ(ecosystem)	5	392.4	8.7	0.00
p(constant), ψ(PC2 + PC4)	4	392.5	8.8	0.00
p(constant), ψ(PC1 + PC4)	4	392.5	8.8	0.00
p(PC3 + PC4), ψ(disturbance)	5	392.6	8.9	0.00
p(constant), ψ(ecosystem + PC2 + PC4)	5	392.6	8.9	0.00
p(constant), ψ(ecosystem)	3	392.6	8.9	0.00
p(ecosystem), ψ(PC2)	4	392.6	8.9	0.00
p(disturbance), ψ(PC2 + PC3 + PC4)	6	392.7	8.9	0.00
p(disturbance + PC3), ψ(constant)	4	392.8	9.1	0.00

p(PC1 + PC3), ψ(disturbance)	5	392.9	9.1	0.00
p(ecosystem + disturbance), ψ(PC1 + PC3)	6	392.9	9.2	0.00
p(disturbance), ψ(PC1 + PC3 + PC4)	6	392.9	9.2	0.00
p(constant), ψ(ecosystem + PC3)	4	393.0	9.3	0.00
p(PC1 + PC3), ψ(PC4)	5	393.2	9.4	0.00
p(PC2 + PC3), ψ(disturbance)	5	393.2	9.5	0.00
p(ecosystem + disturbance), ψ(PC2)	5	393.3	9.5	0.00
p(PC1), ψ(PC3 + PC4)	5	393.3	9.6	0.00
p(PC1 + PC4), ψ(disturbance)	5	393.4	9.7	0.00
p(ecosystem), ψ(PC1 + PC2)	5	393.4	9.7	0.00
p(ecosystem), ψ(PC2 + PC3)	5	393.6	9.9	0.00
p(PC2 + PC4), ψ(disturbance)	5	393.6	9.9	0.00
p(ecosystem + PC2 + PC4), ψ(constant)	5	393.6	9.9	0.00
p(disturbance), ψ(PC1 + PC2 + PC4)	6	393.7	9.9	0.00
p(PC1 + PC2), ψ(disturbance)	5	393.7	10.0	0.00
p(constant), ψ(PC2 + PC3 + PC4)	5	393.7	10.0	0.00
p(PC3), ψ(ecosystem)	4	393.7	10.1	0.00
p(constant), ψ(PC1 + PC3 + PC4)	5	393.8	10.1	0.00
p(ecosystem + disturbance), ψ(PC2 + PC3)	6	393.9	10.2	0.00
p(PC1 + PC2), ψ(ecosystem)	5	393.9	10.2	0.00
p(PC1 + PC4), ψ(ecosystem)	5	393.9	10.2	0.00
p(PC3), ψ(PC1 + PC4)	5	393.9	10.2	0.00
p(constant), ψ(disturbance + PC1 + PC2)	5	393.9	10.2	0.00
p(PC1 + PC2), ψ(PC4)	5	394.0	10.3	0.00
p(PC2), ψ(PC3 + PC4)	5	394.2	10.4	0.00
p(PC2 + PC3), ψ(PC4)	5	394.2	10.5	0.00
p(constant), ψ(PC1 + PC2 + PC4)	5	394.3	10.5	0.00
p(disturbance + PC1 + PC3), ψ(constant)	5	394.4	10.7	0.00
p(ecosystem + disturbance), ψ(PC1 + PC2)	6	394.4	10.7	0.00
p(ecosystem), ψ(PC1 + PC2 + PC3)	6	394.5	10.8	0.00
p(PC1 + PC3 + PC4), ψ(disturbance)	6	394.5	10.8	0.00
p(PC4), ψ(ecosystem)	4	394.5	10.8	0.00
p(PC1 + PC2 + PC3), ψ(ecosystem)	6	394.6	10.8	0.00
p(PC1 + PC3 + PC4), ψ(ecosystem)	6	394.6	10.9	0.00
p(disturbance), ψ(constant)	3	394.6	10.9	0.00
p(PC2 + PC3 + PC4), ψ(disturbance)	6	394.6	10.9	0.00
p(PC2), ψ(PC1 + PC4)	5	394.7	10.9	0.00
p(PC2), ψ(ecosystem)	4	394.8	11.0	0.00
p(constant), ψ(ecosystem + PC2)	4	394.8	11.0	0.00
p(disturbance), ψ(PC1 + PC2 + PC3 + PC4)	7	394.9	11.2	0.00
p(PC1 + PC3), ψ(PC2 + PC4)	6	394.9	11.2	0.00

p(PC1 + PC2 + PC3), ψ(disturbance)	6	394.9	11.2	0.00
p(disturbance + PC3 + PC4), ψ(constant)	5	394.9	11.2	0.00
p(disturbance + PC2 + PC3), ψ(constant)	5	395.0	11.3	0.00
p(PC1), ψ(PC2 + PC3 + PC4)	6	395.1	11.4	0.00
p(constant), ψ(ecosystem + PC2 + PC3)	5	395.2	11.5	0.00
p(PC1 + PC2 + PC3), ψ(PC4)	6	395.3	11.5	0.00
p(PC1 + PC2 + PC4), ψ(disturbance)	6	395.4	11.7	0.00
p(PC1 + PC2), ψ(PC3 + PC4)	6	395.4	11.7	0.00
p(constant), ψ(PC1 + PC2 + PC3 + PC4)	6	395.5	11.8	0.00
p(disturbance), ψ(PC3)	4	395.6	11.9	0.00
p(PC3 + PC4), ψ(ecosystem)	5	395.7	11.9	0.00
p(PC3), ψ(PC1 + PC2 + PC4)	6	395.7	12.0	0.00
p(PC2 + PC3), ψ(ecosystem)	5	395.9	12.2	0.00
p(PC2), ψ(PC1 + PC3 + PC4)	6	395.9	12.3	0.00
p(PC1 + PC2 + PC4), ψ(ecosystem)	6	396.0	12.3	0.00
p(disturbance + PC1), ψ(constant)	4	396.1	12.3	0.00
p(PC2 + PC3), ψ(PC1 + PC4)	6	396.1	12.4	0.00
p(disturbance), ψ(PC2)	4	396.3	12.6	0.00
p(PC1 + PC2 + PC3 + PC4), ψ(disturbance)	7	396.5	12.8	0.00
p(disturbance + PC4), ψ(constant)	4	396.6	12.9	0.00
p(disturbance), ψ(PC1)	4	396.7	12.9	0.00
p(PC2 + PC4), ψ(ecosystem)	5	396.7	12.9	0.00
p(PC1 + PC2 + PC3 + PC4), ψ(ecosystem)	7	396.7	12.9	0.00
p(disturbance + PC2), ψ(constant)	4	396.8	13.1	0.00
p(constant), ψ(constant)	2	396.8	13.1	0.00
p(disturbance), ψ(PC2 + PC3)	5	397.4	13.6	0.00
p(disturbance), ψ(PC1 + PC3)	5	397.7	14.0	0.00
p(PC2 + PC3 + PC4), ψ(ecosystem)	6	397.9	14.2	0.00
p(disturbance + PC1 + PC4), ψ(constant)	5	398.1	14.3	0.00
p(constant), ψ(PC3)	3	398.1	14.4	0.00
p(PC3), ψ(constant)	3	398.1	14.4	0.00
p(PC1), ψ(constant)	3	398.2	14.5	0.00
p(PC4), ψ(constant)	3	398.3	14.5	0.00
p(disturbance + PC1 + PC2), ψ(constant)	5	398.3	14.5	0.00
p(disturbance), ψ(PC1 + PC2)	5	398.4	14.7	0.00
p(constant), ψ(PC2)	3	398.5	14.8	0.00
p(constant), ψ(PC1)	3	398.6	14.8	0.00
p(disturbance + PC2 + PC4), ψ(constant)	5	398.8	15.1	0.00
p(PC2), ψ(constant)	3	398.9	15.1	0.00
p(disturbance), ψ(PC1 + PC2 + PC3)	6	399.5	15.8	0.00
p(PC3 + PC4), ψ(constant)	4	399.5	15.8	0.00

p(PC1 + PC3), ψ(constant)	4	399.5	15.8	0.00
p(PC1 + PC4), ψ(constant)	4	399.8	16.1	0.00
p(constant), ψ(PC2 + PC3)	4	399.9	16.2	0.00
p(constant), ψ(PC1 + PC3)	4	399.9	16.2	0.00
p(PC2 + PC3), ψ(constant)	4	400.2	16.5	0.00
p(PC1 + PC2), ψ(constant)	4	400.2	16.5	0.00
p(PC2 + PC4), ψ(constant)	4	400.3	16.6	0.00
p(constant), ψ(PC1 + PC2)	4	400.3	16.6	0.00
p(PC1 + PC3 + PC4), ψ(constant)	5	401.1	17.4	0.00
p(PC1 + PC4), ψ(PC3)	5	401.2	17.4	0.00
p(PC3 + PC4), ψ(PC1)	5	401.3	17.6	0.00
p(PC3 + PC4), ψ(PC2)	5	401.4	17.6	0.00
p(PC1 + PC3), ψ(PC2)	5	401.4	17.6	0.00
p(PC4), ψ(PC2 + PC3)	5	401.4	17.7	0.00
p(PC1), ψ(PC2 + PC3)	5	401.4	17.7	0.00
p(PC4), ψ(PC1 + PC3)	5	401.4	17.7	0.00
p(PC1 + PC2 + PC3), ψ(constant)	5	401.6	17.8	0.00
p(PC2 + PC3 + PC4), ψ(constant)	5	401.6	17.9	0.00
p(PC1 + PC2), ψ(PC3)	5	401.6	17.9	0.00
p(PC1 + PC4), ψ(PC2)	5	401.6	17.9	0.00
p(constant), ψ(PC1 + PC2 + PC3)	5	401.7	17.9	0.00
p(PC3), ψ(PC1 + PC2)	5	401.8	18.0	0.00
p(PC1 + PC2 + PC4), ψ(constant)	5	401.8	18.1	0.00
p(PC4), ψ(PC1 + PC2)	5	401.8	18.1	0.00
p(PC2 + PC3), ψ(PC1)	5	402.0	18.3	0.00
p(PC2), ψ(PC1 + PC3)	5	402.0	18.3	0.00
p(PC1 + PC3 + PC4), ψ(PC2)	6	402.9	19.3	0.00
p(PC1 + PC4), ψ(PC2 + PC3)	6	403.1	19.3	0.00
p(PC1 + PC2 + PC3 + PC4), ψ(constant)	6	403.1	19.4	0.00
p(PC1 + PC2 + PC4), ψ(PC3)	6	403.2	19.5	0.00
p(PC3 + PC4), ψ(PC1 + PC2)	6	403.2	19.5	0.00
p(PC4), ψ(PC1 + PC2 + PC3)	6	403.3	19.5	0.00
p(PC2 + PC3 + PC4), ψ(PC1)	6	403.4	19.7	0.00
p(PC2 + PC4), ψ(PC1 + PC3)	6	403.6	19.8	0.00

APPENDIX B

FULL RESULTS FOR *S. GRAMMICUS* DETECTION AND OCCUPANCY

Table 5. List of Models Run for *S. grammicus*, (p = detection, ψ = occupancy)

Model	df	AICc	Δ AICc	Weight
p(PC2 + PC3), ψ(PC1 + PC4)	6	286.5	0	0.25
p(PC2 + PC3), ψ(PC1)	5	287.3	0.7	0.18
p(PC2 + PC3 + PC4), ψ(PC1)	6	289.0	2.5	0.07
p(PC2 + PC3), ψ(PC4)	5	289.5	2.9	0.06
p(PC2 + PC3), ψ(ecosystem)	5	289.4	2.9	0.06
p(disturbance + PC2 + PC3), ψ(constant)	5	289.7	3.1	0.05
p(PC2 + PC3), ψ(constant)	4	290.1	3.5	0.04
p(ecosystem + PC2 + PC3), ψ(constant)	5	290.8	4.3	0.03
p(PC2 + PC3), ψ(ecosystem + disturbance)	6	291.2	4.7	0.02
p(PC2 + PC3 + PC4), ψ(ecosystem)	6	291.5	4.9	0.02
p(PC2 + PC3), ψ(disturbance)	5	291.5	4.9	0.02
p(PC2 + PC3 + PC4), ψ(constant)	5	291.7	5.1	0.02
p(PC1 + PC2 + PC3), ψ(PC4)	6	291.7	5.1	0.02
p(PC1 + PC2 + PC3), ψ(ecosystem)	6	291.7	5.2	0.02
p(PC2), ψ(PC1 + PC4)	5	291.9	5.4	0.02
p(PC1 + PC2 + PC3), ψ(constant)	5	292.2	5.6	0.02
p(PC2), ψ(PC1 + PC3 + PC4)	6	293.1	6.6	0.01
p(PC2 + PC3 + PC4), ψ(disturbance)	6	293.2	6.6	0.01
p(PC1 + PC2 + PC3), ψ(disturbance)	6	293.6	7.1	0.01
p(PC1 + PC2 + PC3 + PC4), ψ(ecosystem)	7	293.8	7.2	0.01
p(PC1 + PC2 + PC3 + PC4), ψ(constant)	6	293.8	7.2	0.01
p(PC2), ψ(PC1 + PC3)	5	293.9	7.4	0.01
p(PC2), ψ(ecosystem)	4	294.7	8.2	0.00
p(PC2), ψ(constant)	3	295.2	8.7	0.00
p(PC1 + PC2 + PC3 + PC4), ψ(disturbance)	7	295.3	8.8	0.00
p(PC2 + PC4), ψ(PC1 + PC3)	6	295.3	8.8	0.00
p(PC2), ψ(PC3 + PC4)	5	295.4	8.9	0.00
p(disturbance + PC2), ψ(constant)	4	295.6	9.1	0.00
p(PC1 + PC2), ψ(PC4)	5	296.2	9.6	0.00
p(PC1 + PC2), ψ(ecosystem)	5	296.5	9.9	0.00
p(PC2), ψ(ecosystem + disturbance)	5	296.6	10.1	0.00
p(PC2 + PC4), ψ(ecosystem)	5	296.9	10.3	0.00
p(PC2), ψ(disturbance)	4	296.9	10.3	0.00
p(PC2 + PC4), ψ(constant)	4	296.9	10.4	0.00
p(PC3), ψ(PC1 + PC4)	5	296.9	10.4	0.00
p(PC1 + PC2), ψ(constant)	4	297.2	10.6	0.00
p(ecosystem + PC2), ψ(constant)	4	297.3	10.8	0.00
p(PC1 + PC2), ψ(PC3 + PC4)	6	297.5	10.9	0.00

p(disturbance + PC2 + PC4), ψ(constant)	5	297.6	11.1	0.00
p(disturbance + PC1 + PC2), ψ(constant)	5	297.9	11.3	0.00
p(constant), ψ(PC1 + PC4)	4	298.0	11.5	0.00
p(PC1 + PC2), ψ(ecosystem + disturbance)	6	298.5	11.9	0.00
p(PC1 + PC2), ψ(PC3)	5	298.5	11.9	0.00
p(ecosystem + PC3), ψ(constant)	4	298.6	12.1	0.00
p(PC1 + PC2 + PC4), ψ(ecosystem)	6	298.7	12.2	0.00
p(PC2 + PC4), ψ(disturbance)	5	298.7	12.2	0.00
p(PC2 + PC4), ψ(ecosystem + disturbance)	6	298.8	12.3	0.00
p(PC1 + PC2), ψ(disturbance)	5	298.9	12.3	0.00
p(ecosystem + PC1 + PC2), ψ(constant)	5	298.9	12.4	0.00
p(PC1 + PC2 + PC4), ψ(constant)	5	299.0	12.5	0.00
p(PC3), ψ(PC1 + PC2 + PC4)	6	299.0	12.5	0.00
p(constant), ψ(PC1 + PC3 + PC4)	5	299.1	12.6	0.00
p(ecosystem + PC2 + PC4), ψ(constant)	5	299.1	12.6	0.00
p(constant), ψ(PC1)	3	299.4	12.8	0.00
p(constant), ψ(disturbance + PC1 + PC4)	5	299.4	12.9	0.00
p(ecosystem + PC1 + PC3), ψ(constant)	5	299.5	13.0	0.00
p(disturbance), ψ(PC1 + PC4)	5	299.6	13.1	0.00
p(ecosystem), ψ(PC1 + PC4)	5	299.6	13.1	0.00
p(PC3), ψ(ecosystem)	4	299.8	13.2	0.00
p(ecosystem + PC3 + PC4), ψ(constant)	5	299.8	13.3	0.00
p(constant), ψ(disturbance + PC1)	4	299.9	13.4	0.00
p(constant), ψ(PC1 + PC2 + PC4)	5	300.1	13.5	0.00
p(constant), ψ(ecosystem + PC1 + PC4)	5	300.2	13.7	0.00
p(PC1 + PC2 + PC4), ψ(PC3)	6	300.4	13.8	0.00
p(ecosystem), ψ(PC1)	4	300.5	13.9	0.00
p(constant), ψ(PC1 + PC3)	4	300.5	13.9	0.00
p(constant), ψ(ecosystem)	3	300.5	14.0	0.00
p(ecosystem), ψ(PC1 + PC3 + PC4)	6	300.6	14.0	0.00
p(PC3), ψ(PC1 + PC2)	5	300.6	14.0	0.00
p(constant), ψ(disturbance + PC1 + PC3)	5	300.6	14.1	0.00
p(disturbance), ψ(PC1)	4	300.7	14.2	0.00
p(disturbance), ψ(PC1 + PC3 + PC4)	6	300.8	14.2	0.00
p(PC3 + PC4), ψ(PC1)	5	300.8	14.2	0.00
p(constant), ψ(PC4)	3	300.8	14.2	0.00
p(PC1 + PC2 + PC4), ψ(disturbance)	6	300.9	14.3	0.00
p(constant), ψ(ecosystem + PC1)	4	300.9	14.3	0.00
p(constant), ψ(ecosystem + PC3)	4	300.9	14.4	0.00
p(ecosystem + disturbance), ψ(PC1 + PC4)	6	301.1	14.6	0.00
p(constant), ψ(PC1 + PC2 + PC3 + PC4)	6	301.2	14.7	0.00

p(constant), ψ(ecosystem + PC4)	4	301.3	14.8	0.00
p(constant), ψ(PC1 + PC2)	4	301.4	14.8	0.00
p(ecosystem), ψ(PC1 + PC3)	5	301.4	14.9	0.00
p(PC3), ψ(ecosystem + disturbance)	5	301.5	14.9	0.00
p(PC3), ψ(constant)	3	301.5	14.9	0.00
p(ecosystem), ψ(PC4)	4	301.5	14.9	0.00
p(constant), ψ(ecosystem + PC1 + PC3)	5	301.6	15.0	0.00
p(ecosystem + disturbance), ψ(PC1)	5	301.6	15.1	0.00
p(ecosystem), ψ(PC1 + PC2 + PC4)	6	301.6	15.1	0.00
p(disturbance), ψ(PC1 + PC2 + PC4)	6	301.7	15.2	0.00
p(constant), ψ(ecosystem + PC2)	4	301.7	15.2	0.00
p(disturbance), ψ(PC1 + PC3)	5	301.8	15.3	0.00
p(constant), ψ(PC3 + PC4)	4	301.9	15.4	0.00
p(constant), ψ(disturbance + PC1 + PC2)	5	301.9	15.4	0.00
p(constant), ψ(ecosystem + PC3 + PC4)	5	301.9	15.4	0.00
p(PC3 + PC4), ψ(ecosystem)	5	301.9	15.4	0.00
p(PC1 + PC3), ψ(ecosystem)	5	301.9	15.4	0.00
p(ecosystems), ψ(ecosystems)	4	302.0	15.5	0.00
p(constant), ψ(constant)	2	302.0	15.5	0.00
p(constant), ψ(ecosystem + PC2 + PC3)	5	302.1	15.6	0.00
p(ecosystem), ψ(constant)	3	302.2	15.7	0.00
p(disturbance), ψ(ecosystem)	4	302.3	15.7	0.00
p(constant), ψ(ecosystem + disturbance)	4	302.3	15.8	0.00
p(ecosystem + disturbance), ψ(PC1 + PC3)	6	302.4	15.9	0.00
p(ecosystem), ψ(PC1 + PC2)	5	302.4	15.9	0.00
p(PC4), ψ(ecosystem)	4	302.4	15.9	0.00
p(ecosystem), ψ(PC3 + PC4)	5	302.5	15.9	0.00
p(constant), ψ(ecosystem + PC1 + PC2)	5	302.5	15.9	0.00
p(disturbance), ψ(PC4)	4	302.5	15.9	0.00
p(constant), ψ(PC1 + PC2 + PC3)	5	302.6	16.0	0.00
p(PC1 + PC3), ψ(PC4)	5	302.6	16.1	0.00
p(PC1), ψ(ecosystem)	4	302.6	16.1	0.00
p(ecosystem), ψ(PC1 + PC2 + PC3 + PC4)	7	302.6	16.1	0.00
p(disturbance + PC3), ψ(constant)	4	302.7	16.2	0.00
p(constant), ψ(disturbance + PC4)	4	302.7	16.2	0.00
p(PC4), ψ(PC1 + PC3)	5	302.7	16.2	0.00
p(disturbance), ψ(PC1 + PC2)	5	302.8	16.2	0.00
p(constant), ψ(ecosystem + PC2 + PC4)	5	302.8	16.3	0.00
p(PC3 + PC4), ψ(PC1 + PC2)	6	302.8	16.3	0.00
p(PC3), ψ(disturbance)	4	302.8	16.3	0.00
p(constant), ψ(PC2 + PC4)	4	302.8	16.3	0.00

p(disturbance), ψ(PC1 + PC2 + PC3 + PC4)	7	302.9	16.4	0.00
p(ecosystem + PC1 + PC4), ψ(constant)	5	302.9	16.5	0.00
p(ecosystem + PC1), ψ(constant)	4	303.0	16.5	0.00
p(ecosystem + disturbance), ψ(PC4)	5	303.0	16.5	0.00
p(constant), ψ(PC3)	3	303.2	16.7	0.00
p(ecosystem), ψ(PC3)	4	303.2	16.7	0.00
p(ecosystem + disturbance), ψ(constant)	4	303.3	16.7	0.00
p(ecosystem), ψ(PC1 + PC2 + PC3)	6	303.5	16.9	0.00
p(constant), ψ(disturbance)	3	303.5	16.9	0.00
p(ecosystem), ψ(PC2 + PC4)	5	303.5	16.9	0.00
p(disturbance), ψ(constant)	3	303.5	16.9	0.00
p(PC1 + PC3), ψ(constant)	4	303.6	17.0	0.00
p(ecosystem + disturbance), ψ(PC1 + PC2)	6	303.6	17.0	0.00
p(PC4), ψ(PC1 + PC2)	5	303.6	17.1	0.00
p(PC3 + PC4), ψ(constant)	4	303.6	17.1	0.00
p(PC3 + PC4), ψ(ecosystem + disturbance)	6	303.7	17.1	0.00
p(disturbance), ψ(PC3 + PC4)	5	303.7	17.2	0.00
p(PC1 + PC3), ψ(ecosystem + disturbance)	6	303.7	17.2	0.00
p(constant), ψ(disturbance + PC3 + PC4)	5	303.8	17.2	0.00
p(ecosystem), ψ(disturbance)	4	303.8	17.3	0.00
p(ecosystem + PC4), ψ(constant)	4	303.9	17.4	0.00
p(disturbance), ψ(PC1 + PC2 + PC3)	6	303.9	17.4	0.00
p(ecosystem + disturbance), ψ(PC3 + PC4)	6	303.9	17.5	0.00
p(constant), ψ(PC2)	3	304.0	17.5	0.00
p(constant), ψ(PC2 + PC3 + PC4)	5	304.0	17.5	0.00
p(disturbance + PC1 + PC3), ψ(constant)	5	304.1	17.5	0.00
p(ecosystem), ψ(PC2)	4	304.1	17.6	0.00
p(PC1), ψ(PC3 + PC4)	5	304.1	17.6	0.00
p(PC1), ψ(constant)	3	304.1	17.6	0.00
p(ecosystem + disturbance), ψ(PC3)	5	304.1	17.6	0.00
p(PC4), ψ(constant)	3	304.1	17.6	0.00
p(PC1 + PC3 + PC4), ψ(ecosystem)	6	304.2	17.6	0.00
p(PC4), ψ(ecosystem + disturbance)	5	304.2	17.7	0.00
p(PC1), ψ(ecosystem + disturbance)	5	304.4	17.9	0.00
p(PC1 + PC4), ψ(ecosystem)	5	304.5	17.9	0.00
p(constant), ψ(disturbance + PC3)	4	304.5	17.9	0.00
p(ecosystem), ψ(PC2 + PC3 + PC4)	6	304.6	18.0	0.00
p(disturbance), ψ(PC2 + PC4)	5	304.6	18.1	0.00
p(disturbance), ψ(PC3)	4	304.6	18.1	0.00
p(PC1 + PC3), ψ(PC2 + PC4)	6	304.7	18.1	0.00
p(constant), ψ(disturbance + PC2 + PC4)	5	304.8	18.3	0.00

p(PC4), ψ(PC1 + PC2 + PC3)	6	304.8	18.3	0.00
p(disturbance + PC3 + PC4), ψ(constant)	5	304.9	18.3	0.00
p(PC1 + PC3), ψ(disturbance)	5	304.9	18.4	0.00
p(ecosystem + disturbance), ψ(PC2 + PC4)	6	304.9	18.5	0.00
p(PC3 + PC4), ψ(disturbance)	5	305.0	18.5	0.00
p(ecosystem + disturbance), ψ(PC2)	5	305.2	18.6	0.00
p(ecosystem), ψ(PC2 + PC3)	5	305.2	18.7	0.00
p(constant), ψ(PC2 + PC3)	4	305.3	18.8	0.00
p(disturbance), ψ(disturbance)	4	305.4	18.8	0.00
p(disturbance), ψ(PC2)	4	305.5	18.9	0.00
p(constant), ψ(disturbance + PC2)	4	305.5	18.9	0.00
p(PC1 + PC3), ψ(PC2)	5	305.6	19.0	0.00
p(disturbance + PC1), ψ(constant)	4	305.6	19.1	0.00
p(PC4), ψ(disturbance)	4	305.6	19.1	0.00
p(PC3 + PC4), ψ(PC2)	5	305.6	19.1	0.00
p(PC1), ψ(disturbance)	4	305.7	19.1	0.00
p(disturbance + PC4), ψ(constant)	4	305.7	19.1	0.00
p(PC1 + PC3 + PC4), ψ(constant)	5	305.7	19.2	0.00
p(disturbance), ψ(PC2 + PC3 + PC4)	6	305.8	19.3	0.00
p(ecosystem + disturbance), ψ(PC2 + PC3)	6	306.1	19.5	0.00
p(PC1 + PC4), ψ(constant)	4	306.3	19.8	0.00
p(PC1), ψ(PC2 + PC3 + PC4)	6	306.3	19.8	0.00
p(PC1 + PC4), ψ(ecosystem + disturbance)	6	306.4	19.8	0.00
p(constant), ψ(disturbance + PC2 + PC3)	5	306.6	20.1	0.00
p(disturbance), ψ(PC2 + PC3)	5	306.7	20.2	0.00
p(PC1 + PC3 + PC4), ψ(disturbance)	6	307.1	20.6	0.00
p(PC1), ψ(PC2 + PC3)	5	307.5	20.9	0.00
p(PC4), ψ(PC2 + PC3)	5	307.5	20.9	0.00
p(PC1 + PC4), ψ(PC3)	5	307.6	21.1	0.00
p(PC1 + PC3 + PC4), ψ(PC2)	6	307.8	21.2	0.00
p(disturbance + PC1 + PC4), ψ(constant)	5	307.8	21.3	0.00
p(PC1 + PC4), ψ(disturbance)	5	307.8	21.3	0.00
p(PC1 + PC4), ψ(PC2)	5	308.4	21.8	0.00
p(PC1 + PC4), ψ(PC2 + PC3)	6	309.7	23.2	0.00