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Title: Spatial interactions between parrotfishes and implications for species coexistence

Keywords: coexistence, coral reefs, home range, movement, parrotfishes, spatial interaction

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Abstract

Home range behavior is common in animals and mediates species interactions and distributions. We investigated home range behavior and spatial interactions in four common parrotfishes on coral reefs in Bonaire, Caribbean Netherlands, to determine the contributions of spatial interactions to their coexistence. We computed home ranges for females and males of each species and quantified spatial overlap (i.e., static interaction) of co-occurring home range pairs to estimate interaction potential for pairs of individuals. We then analyzed dynamic interactions in simultaneously tracked, spatially co-occurring inter- and intraspecific pairs of parrotfishes to investigate how they interact in shared space. Individuals in inter- and intraspecific pairs of fishes moved mostly independently of each other in shared areas, but we found evidence of avoidance in interspecific pairs sharing the most space. We discuss our findings within the context of parrotfish social behavior to further elucidate the spatial ecology of these functionally important reef fishes.

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Introduction

A home range (HR) is broadly defined as a self-restricted area in which an animal conducts its normal daily activities, and arises from individual movement decisions made by an animal in response to its environment (Nathan *et al.* 2008; Van Moorter *et al.* 2016). HRs exist for many animals, with a broad literature investigating the behaviors that give rise to it (Börger *et al.* 2008). HR characteristics are determined by resource abundances (Haskell *et al.* 2002), the space use of competitors (Wakefield *et al.* 2013; Riotte-Lambert *et al.* 2015), and intrinsic characteristics of the animal (e.g., locomotion and trophic status; Harestad & Bunnell 1979; Nash *et al.* 2015; Tamburello *et al.* 2015). Some animals defend all or a portion of their HRs as territories, when the benefit of doing so outweighs the cost (Brown 1964; Kaufmann 1983). HR and territorial behavior can affect population dynamics and regulation, including by setting upper limits on population size (Newton 1992; López-Sepulcre & Kokko 2005; Wang & Grimm 2007; Wood *et al.* 2012).

Movement and space use can also facilitate species coexistence (reviewed in Schlägel *et al.* 2020). Coexistence is maintained through mechanisms that minimize average fitness differences between organisms (equalizing) or increase the strength of intraspecific competition relative to interspecific competition (stabilizing; Chesson 2000). Spatiotemporal segregation, mediated by animal movement and space use, may act as a stabilizing mechanism that facilitates coexistence of competing species (Berger & Gese 2007; Macandza *et al.* 2012; Papastamatiou *et al.* 2018; Schlägel *et al.* 2020). Yet, studies linking these processes remain relatively limited.

Although trophic resource partitioning has been studied extensively in parrotfishes (Adam *et al.* 2015; Nicholson & Clements 2020, 2021), very little is known about how their movements and space use contribute to niche partitioning and coexistence. Parrotfishes graze on

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epilithic and endolithic microautotrophs, including cyanobacteria, maintaining reef substrates in cropped early successional states (Clements *et al.* 2016; Cissell *et al.* 2019; Nicholson & Clements 2020). Their grazing is, therefore, considered important in facilitating coral settlement and recruitment (Mumby *et al.* 2007). Adult male (terminal phase; TP) parrotfishes of many species defend stable, exclusive territories containing harems of intraspecific females (initial phase; IP) against intraspecific TPs, increasing their spawning success and access to high quality foods (van Rooij *et al.* 1996; Mumby & Wabnitz 2002). Territoriality also contributes to population regulation (López-Sepulcre & Kokko 2005), and could impose spatial constraints on parrotfish foraging that mediate spatial patterns of benthic community assembly (Sandin & McNamara 2012; Welsh & Bellwood 2012). However, studies of parrotfish movement and space-use are often limited to correlating HR size to body size or resource abundance (e.g., Welsh *et al.* 2013; Carlson *et al.* 2017).

In this study, we investigated spatial interactions among four common Caribbean parrotfishes. Specifically, we tested the hypothesis that parrotfishes would avoid one another spatially and/or temporally to reduce competition for shared resources. To test this hypothesis, we estimated HRs for several TPs and IPs of each species to quantify differences in space use and the spatial overlap (i.e., static interaction) of co-occurring TP pairs (inter- and intraspecific) and haremic pairs (TP and IP). Furthermore, we analyzed the movements of simultaneously tracked interspecific pairs of TP parrotfishes and intraspecific haremic TP-IP pairs to quantify dynamic interactions between these fishes in shared space. Finally, we conducted behavioral observations to provide context for our findings.

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Material and methods

Study sites and data collection

We conducted our study in June-July 2021 at two fringing coral reef sites on the leeward coast of Bonaire, Caribbean Netherlands: Aquarius and Invisibles. These sites are characterized by relatively high coral cover and low macroalgal cover (Manning & McCoy 2021). The abundance and biomass of different fish groups, including parrotfishes, is higher on Bonaire's coral reefs relative to more heavily fished reefs in the Eastern Caribbean (Steneck *et al.* 2019). This is likely due to fisheries management efforts, including spear gun bans (1971), the establishment of no fishing areas (2008), bans on parrotfishes catches (2010), and fish trap phase-outs (2010; Jackson et al. 2014).

At each site, we collected two separate datasets: (1) GPS tracking and behavioral observations of several individuals, one by one, to estimate HRs, quantify static interactions, and explore the role of agonistic behavior in driving these patterns; and (2) simultaneous GPS tracking of two neighboring parrotfishes to investigate dynamic interactions between spatially co-occurring individuals. GPS tracks were recorded using a Garmin GPSMAP 78sc by a snorkeler remaining at the surface just above the tracked individual while a SCUBA diver monitored its behavior below the surface (see below). Divers acclimated fish to their presence for ~ 2 mins and subsequently observed fish behavior from ~ 2 m to avoid influencing behavior. Snorkelers were well above the fish during GPS tracking (5 m or more) and were unlikely to have influenced fish behavior. Parrotfishes in Bonaire are also likely habituated to divers because of spearfishing bans (Jackson *et al.* 2014) and a thriving dive tourism industry.

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Space use and static interactions

At each study site, we tracked several TP and IP individuals of four common parrotfishes, *Scarus taeniopterus*, *Sc. vetula*, *Sparisoma aurforenatum*, and *Sp. viride*, for ~20 mins (Appendix S1: Table S1). We tracked all territorial TP fishes within predetermined ~1,000 m^2 plots at each study site. We also tracked haremic IPs from different territories for all species. We verified that our tracking duration was sufficient to capture HR behavior by conducting visual assessments of stationarity (Benhamou 2014; Appendix S1: Figure S1). Additionally, individual parrotfish are known to use these diurnal (i.e., daytime) HRs for extended periods of time (i.e., months; van Rooij *et al.* 1996).

For each individual, we computed HR and core areas (CA), defined as the areas within the 95% and 50% cumulative isopleths of the utilization distribution (UD), respectively, using movement-based kernel density estimation (Benhamou 2011). We quantified the spatial overlap of HRs (i.e., static interactions) for intra- and interspecific pairs of spatially co-occurring (i.e., neighboring) TPs using Bhattacharyya's Affinity (BA; Fieberg & Kochanny 2005). We also quantified the spatial overlap of each IP HR with TP HRs, and a given IP was assumed to belong to the TP's harem based on the greatest spatial overlap. The UDs and BAs were computed in the adehabitatHR R package (Calenge 2006).

We used linear models to investigate differences in HR and CA size (log transformed to meet normality and homoscedasticity assumptions; graphically assessed) as a function of site, species, ontogenetic phase, and the interaction of species and phase (Appendix S1: Table S2). We used beta regressions ('betareg' R package v. 3.1.4; Cribari-Neto & Zeileis, 2010) to assess the effects of (1) site and species pairings on static interactions (i.e. spatial overlap between HRs) between spatially co-occurring pairs of TP parrotfishes (Appendix S1: Table S3) and (2) site and

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species on static interactions between haremic TP-IP pairs (Appendix S1: Table S4). For each beta regression analysis, we fit both fixed and variable dispersion models (i.e., precision parameter fixed or allowed to vary as a function of explanatory variables, respectively) of static interaction and used a two-step model selection process to select the best-fit model using likelihood ratio tests (Bayer & Cribari-Neto, 2017). For significant terms in all models, we computed marginal means and performed multiple comparisons with Sidak corrections.

Spatial patterns of agonistic behavior

We concurrently video-recorded the behavior of each TP fish with a GoPro Hero 4 Silver (GoPro, Inc) and analyzed these videos in the behavioral analysis software BORIS (Friard & Gamba 2016). We recorded the duration of all agonistic interactions (agonisms) and species and ontogenetic phase of the interactor. Apparent agonisms for which we were unable to identify the interactor were excluded from analyses. Agonisms lasting less than 1s were scored as 1s. Video times were UTC/GPS-synchronized to estimate where each agonism occurred. We assessed the predictors of agonism frequency with a generalized linear model fit to a negative binomial distribution (Appendix S1: Table S5). We included site, species and interactor identity as fixed effects and the log of observation time as an offset. We assessed the predictors of agonism duration (log transformed to meet the model's assumptions) and the minimum distance between the agonism and HR boundary of the focal fish with a linear mixed model including site, species, and interactor identity (e.g., TP – intraspecific, etc.) as fixed effects and focal fish ID as a random effect (Appendix S1: Tables S6 and S7). We graphically assessed model residuals to confirm that they met model assumptions.

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Simultaneous tracking and dynamic interactions

We investigated dynamic interactions (i.e., the tendency of two animals to move together, to avoid each other or to move independently) between simultaneously tracked pairs of spatially co-occurring TP *Sp. viride* and *Sc. vetula* (Video 1) and pairs of TP and IP *Sp. viride* (Video 2) at both study sites (Appendix S1: Table S8). GPS tracks for these individuals lasted 30.61 ± 2.61 min (mean ± SD, n = 36) and were resampled to achieve synchronized relocations every 5s.

For each interspecific (n = 9) and intraspecific (n = 9) pair, we identified the area of overlap between the two HRs using the 'st_intersection' function in the R package sf (Pebesma 2018). We then contrasted the actual frequency S/T with which both individuals of a given pair were in this shared area, where T is the total number of simultaneous relocations and S is the number of simultaneous relocations for which both individuals were in the shared area, with the theoretical probability IJ/T^2 that both individuals would simultaneously be in the shared area if they moved independently of each other, where I and J are the numbers of locations in the shared area of each of the two individuals, irrespective of the fact that the other individual was or was not in the shared area. We then tested for avoidance or attractance within shared areas by comparing the difference in the observed and theoretical values with a Wilcoxon signed-ranks test. Finally, we investigated the tendency for each pair to move jointly, independently, or avoid one another when simultaneously present within the shared area by computing the dynamic interaction index (Benhamou *et al.* 2014) using the 'IAB' function in the R package wildlifeDI (Long *et al.* 2014).

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Results

Space use and static interactions

Sizes of HR and CAs were dependent upon both the species and phase (Species x Phase, Wald's $\chi^2 = 15.35$, $p = 0.002$ and Wald's $\chi^2 = 7.95$, $p = 0.047$, respectively). *Scarus taeniopterus* had the smallest HRs and CAs of all species, while *Sc. vetula* and *Sp. viride* had the largest (Figure 1). Additionally, TP HRs and CAs were larger than IP HRs and CAs for all species except *Sc. taeniopterus* (Figure 1).

The spatial overlap of co-occurring TP HRs differed by interactor identities (Wald's $\chi^2 = 63.67$, $p < 0.001$). Intraspecific HR overlaps were significantly lower than interspecific ones in *Sc. vetula*, *Sp. aurofrenatum*, and *Sp. viride* (Figure 2). For *Sc. taeniopterus*, no differences between intraspecific overlap and interspecific overlaps with TP *Sp. viride* and TP *Sc. vetula* were found. Intraspecific overlap of TP HRs was particularly low in *Sc. vetula*, *Sp. aurofrenatum*, and *Sp. viride* (0.03 ± 0.01, 0.07 ± 0.02, and 0.04 ± 0.01; mean ± SE; $n = 14$, 25, and 11 pairs, respectively). Not surprisingly, overlaps of haremic TP and IP HRs were high (0.52 ± 0.03, mean ± SE, $n = 41$ pairs), and did not differ by site or species.

Spatial patterns of agonisms

Focal TPs were most frequently agonistic toward IPs and TPs belonging to the same species ($\chi^2 = 160.76$, $p < 0.001$; Figure 3a). Intraspecific agonisms between TPs lasted longer than all other agonisms ($\chi^2 = 260.37$, $p < 0.001$; Figure 3b) and more frequently involved aggressive chases, rather than brief charges or displays (Fisher's Exact Test $p < 0.001$). Intraspecific agonisms between focal TPs and IPs occurred further from the HR boundary than agonisms between other fishes ($\chi^2 = 11.70$, $p = 0.008$; Figure 3c). Intraspecific agonisms

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between TPs occurred 2.66 ± 0.10 m (mean ± SE, n = 150) from HR boundaries. Focal TP *Sc. taeniopterus* engaged in agonisms more frequently than TPs of other species ($\chi^2 = 27.65$, $p < 0.001$; Appendix S1: Figure S2a), and their agonisms occurred closer to HR boundaries ($\chi^2 = 10.13$, $p = 0.017$; Appendix S1: Figure S2b).

Dynamic interactions

The HRs of simultaneously tracked interspecific pairs of TP *Sp. viride* and TP *Sc. vetula* overlapped substantially (0.51 ± 0.05, mean ± SE), providing a strong basis for potential dynamic interactions. However, the frequency of simultaneous relocations of these pairs within shared areas did not differ from the frequency expected for independent movement ($V = 23$, $p = 1$). We found evidence for dynamic interaction in only one pair of TP *Sp. viride* and TP *Sc. vetula* (Appendix S1: Table S9; Video 1). This pair shared the most space (BA = 0.74) and exhibited significant avoidance while moving in shared areas.

The HRs of simultaneously tracked intraspecific pairs of haremic TP and IP *Sp. viride* also overlapped substantially (0.48 ± 0.04, mean ± SE), but also were not found together within the shared area more or less than would be expected with independent movement ($V = 27$, $p = 0.652$). Analyses of intraspecific dynamic interactions did not reveal any clear patterns. We found evidence for avoidance in one pair, attractance in another, and independent movement for the remaining pairs (Appendix S1: Table S9).

Discussion

We quantified spatial interactions among parrotfishes, which act as functionally important grazers in coral reef ecosystems (reviewed in Bonaldo *et al.* 2014), to investigate the

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role movement and space use play in mediating species interactions and coexistence. Males of multiple parrotfish species are known to defend fixed intraspecific territories from other males (van Rooij *et al.* 1996; Mumby & Wabnitz 2002). Here, we demonstrated how agonistic behavior influences spatial interactions among individuals using modern animal tracking techniques. We found strong intraspecific spatial segregation of TPs in three of our four study species (*Sc. vetula*, *Sp. aurofrenatum*, and *Sp. viride*), and moderately strong intraspecific spatial segregation in *Sc. taeniopterus*. The low intraspecific overlap of TP HRs is likely driven by frequent and aggressive agonistic behaviors between intraspecific fish. Such agonisms occurred within 2-3 m of HR boundaries, suggesting that TPs quickly detected intruders within their territories. In a few cases, these agonisms even occurred outside the HR boundary. TP CAs lie almost entirely within these 3m buffer zones (Fig. S3). Thus, TPs likely have near-exclusive access to the resources in these areas.

Interspecific overlap of co-occurring TP HRs was significantly higher than intraspecific overlap of co-occurring TP HRs, but interspecific agonisms between TPs were rarely observed. One possible explanation is that resource partitioning is sufficient to limit interspecific interference competition. Parrotfishes partition resource use along multiple niche axes, including foraging substrates and habitats (Adam *et al.* 2015). Substrates composed of sparse epilithic algae growing atop endolithic communities are considered to be the dominant dietary target of parrotfishes (Bruggemann *et al.* 1994a,b), though some species, primarily *Sparisoma* spp., also graze fleshy macroalgae (Adam *et al.* 2015; Dell *et al.* 2020). Recent research suggests that parrotfishes may partition resource use even more finely, targeting substrates based on taphonomy (i.e., the degree of degradation, from recently dead to highly bio-eroded) and the

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presence of particular epilithic and endolithic communities of microautotrophs, primarily cyanobacteria (Nicholson & Clements 2020, 2021).

Animals can also partition space temporally by avoiding each other when present in shared space, thereby limiting interference competition (e.g., Kortello *et al.* 2007). We detected significant avoidance in a single interspecific pair of TP *Sp. viride* and TP *Sc. vetula*. The home ranges of this pair had the greatest degree of spatial overlap of all simultaneously tracked interspecific pairs of TP *Sp. viride* and TP *Sc. vetula*. Likewise, we detected marginal avoidance in the interspecific pair of TP *Sp. viride* and TP *Sc. vetula* that shared the second most space. It is possible that neighboring individuals of different parrotfish species interact dynamically and avoid one another in shared space dependent upon the degree of HR overlap, but that under typical conditions overlap may be low enough to limit the need for active avoidance. HR sizes are correlated with the abundance and quality of resources (Relyea *et al.* 2000; Saïd *et al.* 2009), including for parrotfishes (Carlson *et al.* 2017), and animals are predicted to increase the size of their HRs in less productive habitats (Harestad & Bunnell 1979). Anthropogenic stressors, including climate change, are leading to rapid and dramatic shifts in the structure and composition of benthic communities on coral reefs (Hughes 1994). As these changes continue, we might expect the potential for dynamic interactions to change as HRs expand and contract in response to shifts in resources. Baseline studies of spatial interactions such as this are, therefore, increasingly important for understanding the effects of climate change on reef fish communities (Manning 2022).

Individuals in most intraspecific pairs of TP and IP *Sp. viride* moved independently of one another in shared space. This was not wholly unexpected since TPs tolerate multiple IPs within their territories (Mumby & Wabnitz 2002); we identified one instance of avoidance and

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one instance of attractance between individuals in intraspecific pairs. Attraction between haremic TPs and IPs likely occurs during courtship or mating, but mating activity peaks much earlier (09:30 h) than we conducted our simultaneous tracks (van Rooij *et al.* 1996). In contrast, avoidance might be expected if CAs of TPs and IPs overlap and there is local competition for resources. We frequently observed apparent dominance interactions between haremic TP and IP parrotfish over access to foraging locations, and intraspecific agonisms between haremic TP and IP occurred primarily in CAs (Fig. S4). However, the CAs of the two members of the pair that avoided one another in shared space did not appear to overlap substantially. Alternatively, the IP that we tracked in this case may have been transitioning from IP to TP, thus incurring more aggression from the focal TP fish. Dynamic interactions between haremic pairs of TP and IP parrotfish may also be complicated by the presence of other IPs in the harem. Future work would benefit from investigations of dynamic interactions between IPs belonging to the same harem. It may also be necessary to investigate dynamic interactions more locally to elucidate the underlying drivers of dynamic interactions within shared space (Long *et al.* 2014).

The results presented here elucidate a few of the mechanisms underlying space use and coexistence in parrotfishes. Specifically, we found that competition drove stronger spatial segregation of TPs belonging to the same species than to different species. Dynamic avoidance does occur between TPs belonging to different parrotfish species, though such interactions are difficult to detect. These interactions may depend on how much space each member of a pair shares, and how shared space is used, but their presence suggests that spatiotemporal segregation can act as a stabilizing mechanism mediating coexistence in parrotfishes. Our results also have implications for understanding the trophic effects of parrotfishes on coral reefs. The effects of grazers on plant and algal communities depends, in part, on spatial variation in grazing pressure

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(Olff & Ritchie 1998). HR behavior and territoriality may concentrate parrotfish grazing and bioerosion locally (Welsh & Bellwood 2012), contributing to spatial heterogeneity in benthic communities. Models suggest that constrained grazing is important for coral larval settlement and recruitment and could affect reef recovery following disturbance (Sandin & McNamara 2012; Eynaud *et al.* 2016). As such, studies of the spatial ecology of parrotfishes, particularly those that investigate spatial interactions, are necessary to provide a more complete understanding of their functional roles on coral reefs.

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Figure Captions

Figure 1: Mean (±SE) home range and core areas for TP (dark) and IP (light) *Sc. taeniopterus*, *Sc. vetula*, *Sp. aurofrenatum*, and *Sp. viride*.

Figure 2: A heatmap of the estimated marginal mean (and asymptotic 95% CI) overlap of the home ranges of neighboring individuals of TP *Sc. taeniopterus*, *Sc. vetula*, *Sp. aurofrenatum*, and *Sp. viride*. Lighter shades of blue indicate less spatial overlap.

Figure 3: Boxplots of (a) the number of agonisms, (b) agonism durations (s), and (c) the distances (m) of those agonisms from the focal home range boundary for agonisms between focal TPs and IPs belonging to either the same species (IP-intraspecific) or another species (IP-interspecific), and TPs belonging either to the same species (TP-intraspecific) or another species (TP-interspecific).

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Figures

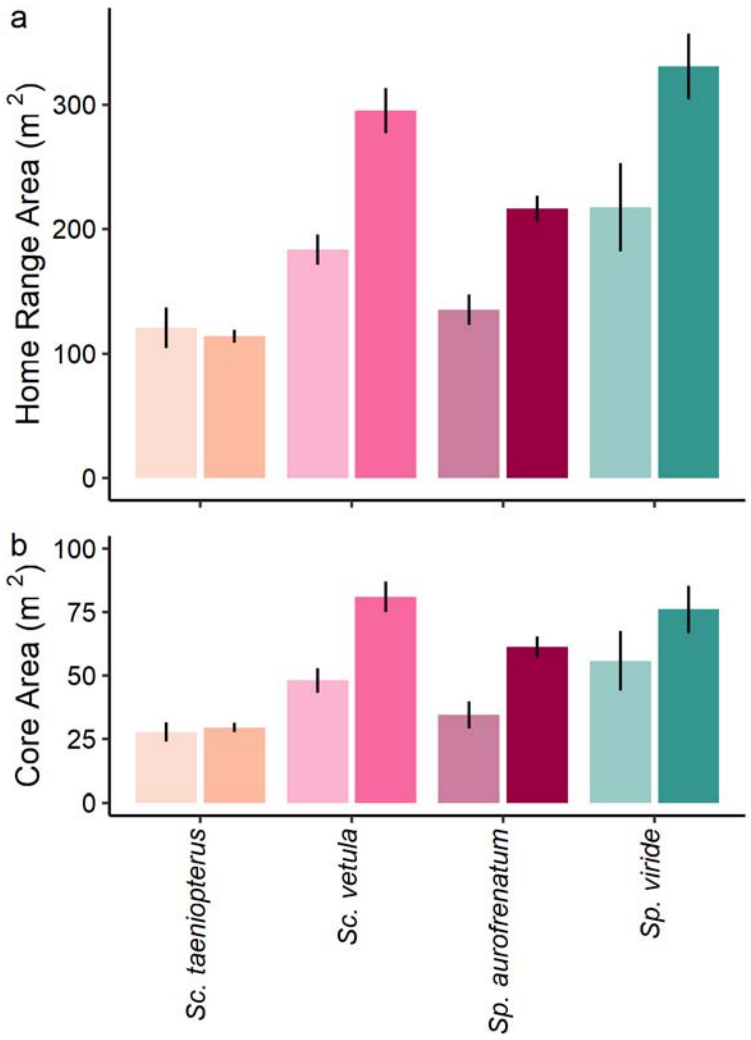

Figure 1

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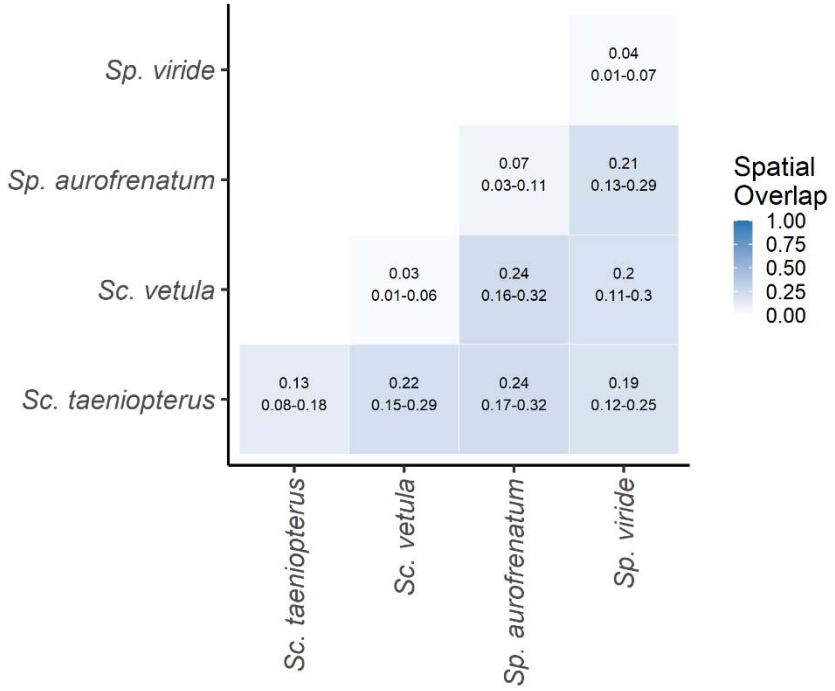

Figure 2

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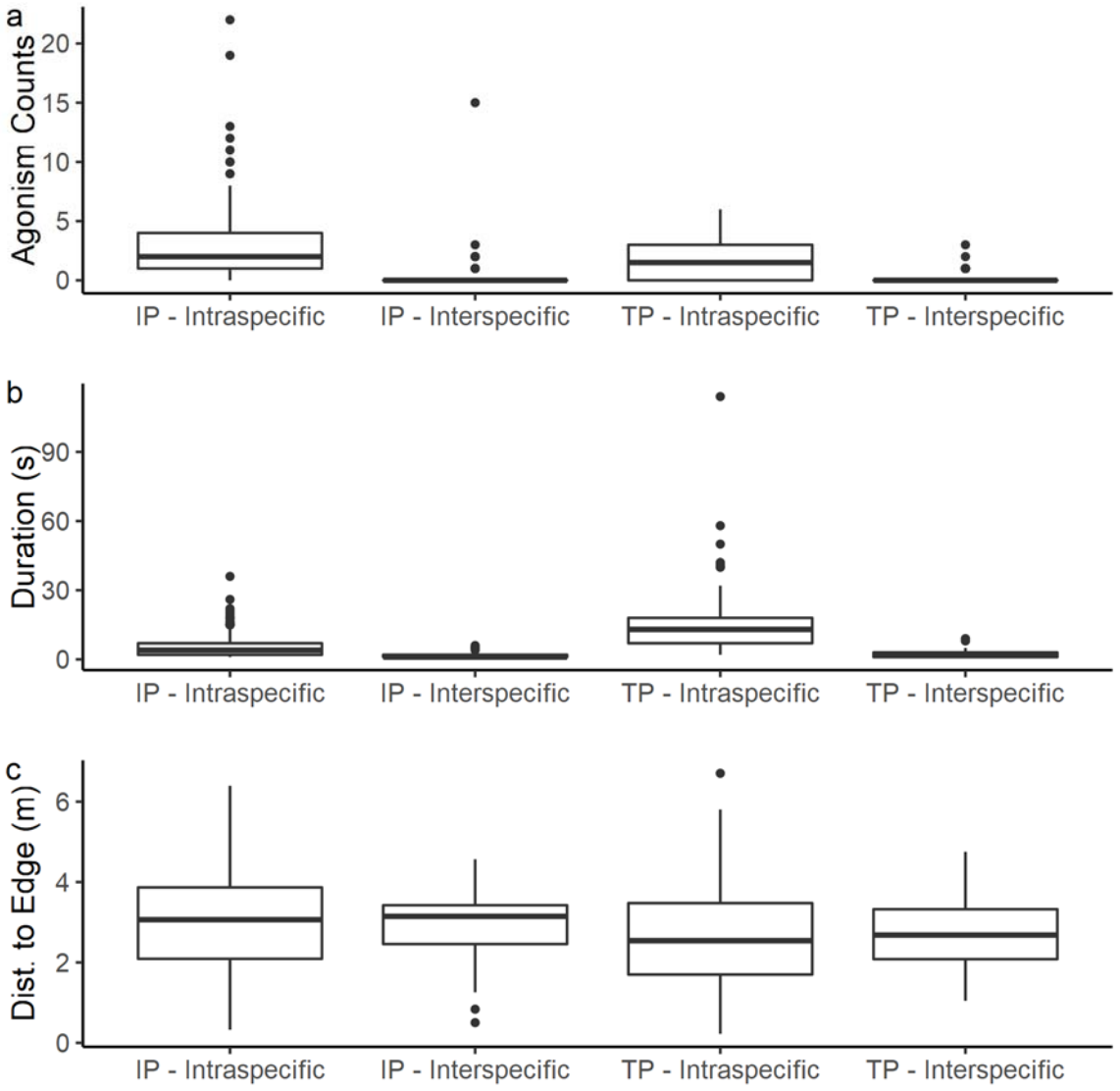

Figure 3