Competitive displacement and agonistic character displacement, or the ghost of interference competition

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ABSTRACT

Interference competition can drive species apart in habitat use through competitive displacement in ecological time and agonistic character displacement (ACD) over evolutionary time. As predicted by ACD theory, sympatric species of rubyspot damselflies (*Hetaerina* spp.) that respond more aggressively to each other in staged encounters differ more in microhabitat use. However, the same pattern could arise from competitive displacement, if dominant species actively exclude subordinate species from preferred microhabitats. The degree to which habitat partitioning is caused by competitive displacement can be assessed with removal experiments. We carried out removal experiments with three species pairs of rubyspot damselflies. With competitive displacement, removing dominant species should allow subordinate species to shift into the dominant species' microhabitat. Instead, we found that species-specific microhabitat use persisted after the experimental removals. Thus, the previously documented association between heterospecific aggression and microhabitat partitioning in this genus is most likely a product of divergence in habitat preferences caused by interference competition in the evolutionary past.

INTRODUCTION

Niche partitioning can arise from competition between species in both ecological and evolutionary time (Price and Kirkpatrick 2009; Pfennig and Pfennig 2012). When the presence of one species narrows the realized niche of another in ecological time, this is referred to as competitive displacement (Debach 1966; Reitz and Trumble 2002). Competitive displacement is reversible in that the affected species' realized niche would expand if the competitor was removed. In contrast, when competition between species causes niche divergence over evolutionary time, this is referred to as character displacement, and removal of the competitor might have no immediate effect (Connell 1980; Martin and Ghalambor 2023).

Competitive displacement can be a source of selection driving character displacement in habitat preferences, but habitat preferences can also diverge between species in response to selection caused by interspecific competition without competitive displacement. All that requires is heritable variation in habitat preferences and for individuals with habitat preferences closer to the other species' mean habitat preference to have lower fitness as a consequence of interspecific competition. Thus, competitive displacement and character displacement can occur together or separately.

Two distinct types of character displacement arising from interspecific competition can drive niche divergence. Ecological character displacement (ECD) is caused by exploitative competition (i.e., resource depletion) and usually leads to reduced resource overlap between species (Schluter 2000; Pfennig and Pfennig 2012). Agonistic character displacement (ACD) is caused by interference competition (e.g., territorial aggression) and involves shifts in traits that affect the rate, intensity or outcome of interspecific encounters (Grether et al. 2009). Both types of character displacement can cause species to diverge in habitat preferences, but the mechanisms of selection differ. With ECD, habitat preferences diverge because of resource depletion where the species overlap (Schluter 2000). With ACD, habitat preferences diverge because interspecific encounters are costly (Grether et al. 2013). ECD is widely regarded as a major driver of niche differentiation between species that compete exploitatively for resources (Schluter 2000; Dayan and Simberloff 2005; Pfennig and Pfennig 2012; but see Stuart and Losos 2013). ACD is best known as a mechanism of divergence between species in competitor recognition (Grether et al. 2009, 2017; Seddon and Tobias 2010; Pasch et al. 2017; Moran and Fuller 2018*a*, 2018*b*), but it could also be an important cause of habitat divergence, particularly in territorial species (Grether et al. 2013; McEachin et al. 2021).

Although interference competition has often been inferred to be the cause of species replacements along elevational and habitat gradients (Heller 1971; Cody and Walter 1976; Schoener 1983; Robinson and Terborgh 1995; Jankowski et al. 2010, 2012; Freeman et al. 2019; Patterson and Drury 2023), the types of manipulative field experiments required to distinguish competitive displacement from ACD are rarely done. Most such experiments that have been published implicate competitive displacement (e.g., (Reed 1982; Garcia 1983; Ebersole 1985; Robertson and Gaines 1986; Ziv et al. 1993; Robertson 1996; Martin and Martin 2001; Stewart et al. 2002; Harmon et al. 2007; Pasch et al. 2013; Edgehouse et al. 2014; Eurich et al. 2018; Martin and Ghalambor 2023), but this could reflect a longstanding bias against publishing negative results. Offering character displacement as an explanation for negative results of competition experiments is what Connell (1980) derisively referred to as invoking the “Ghost of Competition Past”. As Connell (1980) argued, other types of evidence are required to build a convincing case for character displacement. Here we present the results of field experiments to test for competitive displacement in a system for which the requisite evidence already exists (i.e., negative results would implicate ACD).

Interspecific territoriality is a form of interference competition in which individuals of different species compete over space. Quite common in vertebrates (e.g., Orians and Willson 1964; Myrberg and Thresher 1974; Wolff et al. 1983; Shimoyama 1999; Maruyama et al. 2010; Suwanvecho and Brockelman 2012; Benson and Patterson 2013; Harris and Siefferman 2014; Cowen et al. 2020; Drury et al. 2020), interspecific territoriality also occurs in certain invertebrate taxa, including the insect order Odonata (damselflies and dragonflies). Some instances of interspecific territoriality in Odonata might be maladaptive byproducts of intraspecific territoriality (Singer 1989; Schultz and Switzer 2001; Tynkkynen et al. 2004), but in rubyspot damselflies (*Hetaerina* spp.) it appears to be an adaptive response to reproductive interference (Drury et al. 2015, 2019; Grether et al. 2020). Male rubyspot damselflies compete for territories in areas with flowing water and submerged vegetation where females oviposit (Johnson 1963; Córdoba-Aguilar et al. 2009; Guillermo-Ferreira and Del-Claro 2011). Territorial fights are energetically demanding and losers are evicted (Córdoba-Aguilar and Cordero-Rivera 2005). Males recognize females using visual cues and the females of most sympatric species of *Hetaerina* look very similar (Drury et al. 2015, 2019; Grether et al. 2015). Consequently, males try to mate with heterospecific females, resulting in local mate competition between species (Drury et al. 2015; Grether et al. 2020). Territory holders respond more aggressively to male intruders of species with which they compete more intensely for females (Drury et al. 2015; Grether et al. 2020). Nevertheless, territorial fights are costly and species that overlap more in microhabitat use fight more frequently (McEachin et al. 2021). Thus, this is a system in which selection would be expected to cause the habitat preferences of sympatric species to diverge.

Sympatry-allopatry comparison is the canonical method for detecting character displacement in morphology and coloration (Brown Jr. and Wilson 1956), but this is not a suitable method for detecting character displacement in habitat preferences due to an inherent bias toward finding greater habitat differences between species in allopatry than sympatry (Figure 1). This can be understood by considering that, unlike phenotypic traits that are measured on the organism itself, habitat preferences are usually inferred from habitat use, which is constrained by habitat availability. Species with partially overlapping geographic ranges tend to overlap in habitats that are suitable for both species and to occupy different habitats where they do not overlap (Martin and Ghalambor 2023). All habitats at sympatric sites are available to both species, while the habitats at allopatric sites are only available to one species. Consequently, the null expectation is for sympatric species to be more similar in habitat use than allopatric species (Figure 1). Selection could potentially counteract this bias sufficiently to generate a geographic pattern of greater habitat differences in sympatry than allopatry, and cases in which that pattern has been found may be fine examples of character displacement. But when habitat differences between allopatric sites exceed the range of habitats available in sympatry, as must often be the case, there is little scope for selection to generate the predicted pattern of greater species differences in sympatry.

Confusingly, some researchers use the term ‘character displacement’ to refer to the pattern of greater species differences in sympatry than allopatry, but most researchers use it to refer to a category of evolutionary processes, and it is well known that those processes can produce other geographic patterns (Schluter 2000; Pfennig and Pfennig 2012; Grether 2018). To test for ACD in the habitat preferences of rubyspot damselflies, McEachin et al. (2021) tested for a predicted pattern of variation among sympatric populations of 10 species. Specifically, they collected data on species differences in territory microhabitat and the responses of territory holders to heterospecific intruders in 25 pairs of sympatric populations. As would be expected if habitat preferences diverged through ACD, species that responded more aggressively to each other differed more in territory microhabitat (McEachin et al. 2021). However, the same pattern could be caused by competitive displacement, if some species are dominant and exclude others from preferred microhabitats (McEachin et al. 2021).

To test for competitive displacement, we carried out removal experiments with three of the sympatric species studied by McEachin et al. (2021). If species differences in microhabitat are due to competitive displacement, removal of dominant species should allow subordinate species to settle where they were previously excluded and shift in microhabitat use toward dominant species (Pasch et al. 2013; Eurich et al. 2018). We did not have a priori knowledge of which species of *Hetaerina* are dominant, and in any case if males of only one species were removed, territory holders of the unremoved species would continue defending their territories against newcomers, thereby biasing the outcome in favor of newcomers settling in the microhabitat of the removed species (i.e., in favor of the competitive displacement hypothesis). Instead, we removed all territory holders of both species from selected sections of river and monitored resettlement of these initially competitor-free zones. New males were free to settle in removal sections without interference from established territory holders of either species. To examine how this temporary respite from interference competition affected microhabitat use, we compared the species differences in microhabitat prior to removal to that during the early resettlement period. This experimental design is similar to classical succession experiments in which multiple species of sessile organisms were removed (or clean substrate was introduced) to gain insight into the mechanisms that structure ecological communities, including interference competition (e.g., Sousa 1979).

MATERIAL AND METHODS

Removal experiments

We successfully carried out removal experiments at three sites, each with a different focal species pair, in Costa Rica in 2016 and 2017 (Table 1). (At a fourth site, the experiment was aborted because of heavy rain and flooding.) River transects 200-300 m in length, spanning the river and both banks, were marked at 1-m intervals with numbered flags. We marked all of the males in the transects individually using paint pens (Anderson et al. 2011) and released them where they were captured. Starting > 1 week prior to the removals, two to four observers walked along the transects between 0900 and 1700 h recording the locations of marked males to the nearest 0.1 m using hand-held computers. Males were classified as territory holders if they perched repeatedly in the same location (± 2 m) close to the surface of the water (< 1 m) on at least two consecutive days (Anderson and Grether 2010). Damselfly territories do not have discrete boundaries, but prior to the experimental removals, the area within which individual territory holders could fly and perch without being attacked by neighboring territory holders ranged in size from ca. 4 to 9 m^2. In narrow sections of river (< 3 m) a male's territory could span both banks, but in wider sections a transverse line from one bank to the other could cross the territories of multiple males. The transects were divided into sections and removals were done in every other section (4-6 removal sections per site; Table 1). All *Hetaerina* spp. territory holders in removal sections were captured with aerial nets and released on the same river > 100 m above or below the transect, which was sufficient to keep them from returning during the experiment. We erred on the side of removing males whose territorial status was unclear, but females and males without territories were not removed. We continued marking new males and recording the locations of marked males for 1 week post removal. The decision to monitor post-removal settlement for 1 week was based on our knowledge of the study system and the goal of the experiment, which was to document territory settlement in the absence of interference competition. Stopping much sooner would not have allowed sufficient time to document territory settlement; it takes at least 2 days to determine whether a male is a territory holder, and we expected the removal sections to be settled gradually. Continuing to monitor settlement for longer than necessary would have defeated the purpose of the experiment because as occupancy increased further, later settlers would have fought with early settlers.

Microhabitat measurements

We measured the same four microhabitat variables as McEachin et al. (2021): stream width, current speed, canopy cover, and perch height. Stream width (to 0.1 m) and current speed were recorded at 2-m intervals and overstory canopy cover was recorded at 5-m intervals along the transects. Current speed was assessed visually on a 5-point ordinal scale, with 0 for “still”, 1 for “slow” (no waves), 2 for “wavy” (standing waves), 3 for “rippling” (interfering waves), and 4 for “turbulent” water (breaking waves), near both banks and in the middle of the river. A concave spherical densiometer (Forestry Suppliers, Inc.) was used to measure percent canopy cover in the middle and near both banks where the river was $\geq$ 10 m wide, or near both banks where the river was 3-10 m wide, or in the middle where the river was < 3 m wide.

Horizontal coordinates along the transect were used to obtain mean values of stream width, current speed, and canopy cover for each territory holder by interpolation.

Data analysis

To examine whether territories in the removal sections differed in microhabitat from those outside the removal sections, we constructed multivariate linear models with the microhabitat variables as the dependent variables and location (inside versus outside) as a categorical predictor variable.

Euclidean distances in microhabitat space (i.e., the four-dimensional space defined by the microhabitat variables) were used to quantify differences between species before and after the experimental removals. We used the same metric to test the prediction that one species at each site shifted toward the other species' microhabitat during the resettlement period. In principle, this approach might detect species differences and shifts in microhabitat that would not be detected by analyzing the microhabitat variables separately. To weight the four microhabitat variables equally, they were converted to z-scores by subtracting the site mean and dividing by the site standard deviation. Euclidean distances between territory holders in microhabitat space (henceforth, "distances") were calculated using the z-scores.

Each territory holder contributed two data points to the analysis of species differences in microhabitat: a mean distance to conspecific territory holders and a mean distance to heterospecific territory holders. Non-parametric Wilcoxon paired tests were used to compare the conspecific and heterospecific distance distributions because the data were not normally distributed. For testing the competitive displacement prediction that one species at each site shifted toward the other species' microhabitat, each new territory holder in the removal sections contributed one data point: a mean distance to heterospecific territory holders that were present before the removals. Non-parametric Wilcoxon two-sample tests were used to compare those mean distances to the distribution of mean distances between territory holders of the two species before the removals. To account for testing the prediction twice at each site (i.e., once for each species), the *p*-values were adjusted using Holm's method, which is also known as the sequential Bonferroni method (Holm 1979; Hochberg and Benjamin 1990). In practice, however, the results were unaffected by this adjustment at $\alpha = 0.05$.

For an overall test of the effect of the experimental removals on the species difference in microhabitat, data from all sites were combined and a linear mixed-effects model was fit with the 'lmer' function in R package 'lme4' (version 1.1-34). To meet model assumptions, log Euclidian distance was used as the dependent variable. The model's fixed effect terms were species comparison (i.e., conspecific vs. heterospecific), period (i.e., pre- vs. post-removal) and their interaction, and the random effect terms were site and individual. Thus, the model took into account that each territory holder contributed two values (mean distances to conspecifics and heterospecifics) and also the nesting of individuals within sites.

The data analysis was carried out in R version 4.2.2 (The R Foundation for Statistical Computing).

RESULTS

Territories in the removal sections did not differ in microhabitat from those outside the removal sections before or after the experimental removals, at any of the three sites (multivariate linear models, before removal: site GO01 $t = 0.85$, $p = 0.4$; site MV05 $t = 0.91$, $p = 0.4$; site RT02 before removal, $t = 1.02$, $p = 0.3$; after removal: site GO01 $t = 0.12$, $p = 0.9$; site MV05 $t = 0.18$, $p = 0.9$; site RT02 $t = -1.01$, $p = 0.3$).

Males began settling in the removal sections almost immediately, and the number of new territory holders continued increasing for the duration of the experiment (Figure S1). The number of new territory holders varied, but in none of the removal sections did the number of new males of either species reach pre-removal levels by the end of the monitored resettlement period (Table 1). The species differed significantly in territory microhabitat before the experimental removals (Table 2, Figure 2) with one species perching higher and in areas with greater canopy cover than the other at all three sites (Figure 3). The species largely overlapped on the other two microhabitat axes (current speed and stream width; Figure S2). Significant species differences in territory microhabitat were found in the removal sections during the early resettlement period at two sites (Table 2, Figure 2), and the species differences in perch height and canopy cover were in the same directions as prior to the removals at all three sites (Figure 3). Contradicting the competitive displacement hypothesis, none of the species shifted significantly toward the other species' microhabitat during the early resettlement period (Figure 4). With data from the three sites combined, the species difference in microhabitat was highly significant (linear mixed model; $t = 28.95$, $p < 0.0001$) but was not affected by the experimental removals (species comparison×period interaction, $t = -1.44$, $p = 0.15$). The mean distance in microhabitat space between conspecifics decreased between the pre-removal and post-removal periods ($t = -2.87$, $p = 0.02$) but there was no change in the mean distance between heterospecifics ($t = -1.12$, $p = 0.68$). Thus, the only overall effect of the experimental removals was a reduction in the mean microhabitat distance between conspecifics.

DISCUSSION

We carried out removal experiments at three sites to determine whether microhabitat partitioning in rubyspot damselflies is caused by ongoing competitive interactions (i.e., competitive displacement). While the experiments were small in spatial scale and short in duration by vertebrate standards, they were designed for insects with territory sizes in the range of 4-9 square meters and adult life spans of weeks. The species differences in microhabitat were unaffected by the experimental removals at two sites (Figures 2 & 3; Table 2). At a third site, the species did not differ in microhabitat during the resettlement period, but the initial species difference was also smaller than at the other two sites (Figures 2 & 3; Table 2). In no case did one species shift significantly toward the other species' microhabitat (Figure 4). Males that established new territories in the removal sections often perched where conspecific territory holders had perched previously, even though other perches were available (S.M. pers. obs.). However, the mean microhabitat distance between conspecifics decreased somewhat after the experimental removals (Table 2), perhaps because in the absence of competition, males were free to settle according to their species-typical habitat preferences.

Evidently, the differences between these species in microhabitat are the product of differing habitat preferences, not ongoing competitive displacement. This result alone does not implicate agonistic character displacement (ACD) because the species could differ in habitat preferences for a multitude of reasons unrelated to interference competition. However, a previous study of 25 pairs of sympatric populations of rubyspot damselflies showed that microhabitat partitioning increases with the level of heterospecific aggression (McEachin et al. 2021). Heterospecific aggression refers not to the actual rate of interspecific fighting but instead to how aggressively territory holders respond to heterospecific intruders relative to conspecific intruders.

Species differences in microhabitat reduce the frequency of interspecific encounters that result in interspecific fights (McEachin et al. 2021), and thus the positive correlation between microhabitat partitioning and heterospecific aggression is a predictable consequence of selection against interspecific fighting (i.e., ACD). Note that if the direction of causality were reversed, and heterospecific aggression evolved in response to pre-existing species differences in microhabitat, the correlation between microhabitat partitioning and heterospecific aggression would be negative (i.e., species that differ more in microhabitat would be less aggressive to each other). The purpose of carrying out removal experiments on a subset of the same species pairs was to test an alternative hypothesis, namely that the positive correlation arose from dominant species excluding subordinate species from preferred microhabitats. While ACD and competitive displacement are not mutually exclusive processes, and both could have contributed to the species differences in microhabitat, we found no evidence for competitive displacement.

Species sorting (i.e., differential extinction) is another process that could potentially produce a positive correlation between habitat partitioning and heterospecific aggression if interspecific fighting reduced the probability of species co-occurring (Pigot and Tobias 2013; Rybinski et al. 2016; McEachin et al. 2021). The likelihood that species sorting could have generated the geographic pattern documented by McEachin et al. (2021) cannot yet be fully assessed due to a paucity of research on the effects of species interactions at the adult stage on coexistence in Odonata (Svensson et al. 2018; Grether et al. 2023). Nevertheless, interspecific fighting over mating territories seems unlikely to be a strong mechanism of competitive exclusion in this system because there is no parental care, and males do not provide females with resources. In some other groups of territorial damselflies, females have to copulate with the resident male to use the oviposition sites in his territory, but that is not the case in *Hetaerina*

(Grether 1996; Anderson and Grether 2011; Córdoba-Aguilar and González-Tokman 2014). Thus, while interspecific fighting reduces male fitness (Drury and Grether 2014), and species that differ more in microhabitat fight with each other at lower rates (McEachin et al. 2021), it seems very unlikely that the correlation between species differences in microhabitat and heterospecific aggression is the product of differential extinction. By comparison, the hypothesis that the geographic pattern was caused by divergent selection on microhabitat preferences (i.e., ACD) is quite plausible.

The microhabitat differences that have been documented in rubyspot damselflies can be understood to reduce interspecific interference by reducing spatial proximity, either horizontally between different sections or sides of a river (i.e., canopy cover, current speed and stream width) or vertically (i.e., perch height) (Anderson and Grether 2011; McEachin et al. 2021). The species pairs on which we carried out removal experiments tend to perch at different heights and in areas with different amounts of canopy cover (Figure 3). These relatively small differences in habitat preferences could potentially be modified rapidly by selection if the competitive environment changed. For example, if a newly arriving species' canopy cover preference was intermediate relative to the species already present, selection against interspecific fighting might merely reinforce (i.e., narrow) the other species' canopy cover preferences; conversely the disappearance of one species might allow the remaining species' habitat preferences to broaden within their existing environmental tolerances. More generally, however, shifts in habitat use could change the abiotic environment experienced by the animals in ways that cause other types of traits, such as thermal thresholds and morphological traits, to diverge between species (Wcislo 1989; Stuart et al. 2014). In addition to obscuring the original mechanism of divergence, adaptation to the abiotic environment could make habitat preferences harder for selection to modify if the competitive environment changes in the future.

It is worth emphasizing again that competitive displacement and character displacement in habitat preferences are not mutually exclusive processes. The European flycatchers *Ficedula hypoleuca* and *F. albicollis* offer a possible example of competitive displacement leading to evolutionary divergence in habitat preferences. In allopatry both species prefer to breed, reach higher population densities, and achieve higher reproductive success in deciduous forest than coniferous forest (Qvarnström et al. 2009; Veen et al. 2010). In sympatry males of the two species compete for breeding territories and *F. albicollis* usually prevails (Veen et al. 2010). Since arriving on two Baltic islands < 160 years ago, *F. albicollis* males have been outcompeting *F. hypoleuca* males for territories in deciduous forest and forcing them to establish territories in lower quality mixed forest and coniferous forest (Qvarnström et al. 2009; Vallin et al. 2012*a*; Rybinski et al. 2016). The same type of habitat partitioning occurs in an older (post-Pleistocene) contact zone in Central Europe, but aviary experiments showed that *H. hypoleuca* in the old contact zone actually prefer coniferous vegetation (Adamík and Bureš 2007). Competitive displacement presumably occurred when the species first came into contact in Central Europe, just as it is occurring now on the Baltic islands. Thus, the shift in the habitat preference of *H. hypoleuca* seems likely to be an evolved response to competitive displacement in the past (i.e., ACD) but other possible mechanisms have not been ruled out (Qvarnström et al. 2009; Vallin et al. 2012*b*, 2012*a*).

Concluding thoughts

Interspecific aggression is common in many animal groups and could be a major cause of divergence in habitat preferences (Ebersole 1985; Linnell and Strand 2000; Grether et al. 2009, 2017; Rybinski et al. 2016; Jones et al. 2020), but as yet there are few compelling examples. We offer our evidence that interference competition has contributed to species differences in habitat preferences in rubyspot damselflies as one of the clearest examples to date. We also hope this paper serves as a reminder that ignoring the ghost of competition past does not make it disappear. Competition experiments with negative results should only be taken as evidence that competition is not occurring in the present.

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Table 1 Study sites, species pairs, time periods, and number of territory holders outside and inside removal sections.

Site	Latitude Longitude	Species	Month Year	No. of territory holders Outside before removal	Outside after removal	Inside before removal	Inside after removal
GO01	8.643	*H. occisa*	April	12	13	18	12
(4)	-83.1953	*H. fuscoguttata*	2017	8	11	22	8
MV05	10.278	*H. cruentata*	April	20	28	20	13
(6)	-84.8189	*H. capitalis*	2016	20	25	21	5
RT02	10.949	*H. occisa*	May	33	43	45	18
(5)	-85.5116	*H. capitalis*	2016	24	32	65	20

The number of removal sections is shown in parentheses. "Outside" refers to parts of the study transects that were designated as removal sections. As explained in greater detail in the Methods, all *Hetaerina* spp. territory holders were removed from the removal sections and released outside the study transect. Two other *Hetaerina* species (*H. caja* and *H. titia*) were present at low densities at site GO01; no other *Hetaerina* species were present at the other sites.

Table 2. Mean Euclidean distances in microhabitat space between conspecific and heterospecific territory holders pre- and post-removal.

Site	Period	Conspecific Mean	SE	Heterospecific Mean	SE	*n*	*p*
GO01	Pre	2.44	0.05	2.81	0.06	60	<0.0001
	Post	2.11	0.08	3.04	0.08	20	<0.0001
MV05	Pre	2.42	0.05	2.84	0.07	81	<0.0001
	Post	2.26	0.08	2.74	0.14	18	0.0056
RT02	Pre	2.51	0.05	2.61	0.06	167	<0.0001
	Post	2.37	0.10	2.36	0.10	38	0.94

The tabled means are the means of the values plotted in Figure 2, each of which is the mean distance between one territory holder and the other conspecific or heterospecific territory holders present in the same period. Only territories in removal sections were included in post-removal comparisons. The *p*-values are from paired Wilcoxon paired tests comparing conspecific and heterospecific distances; *n* is the number of territory holders.

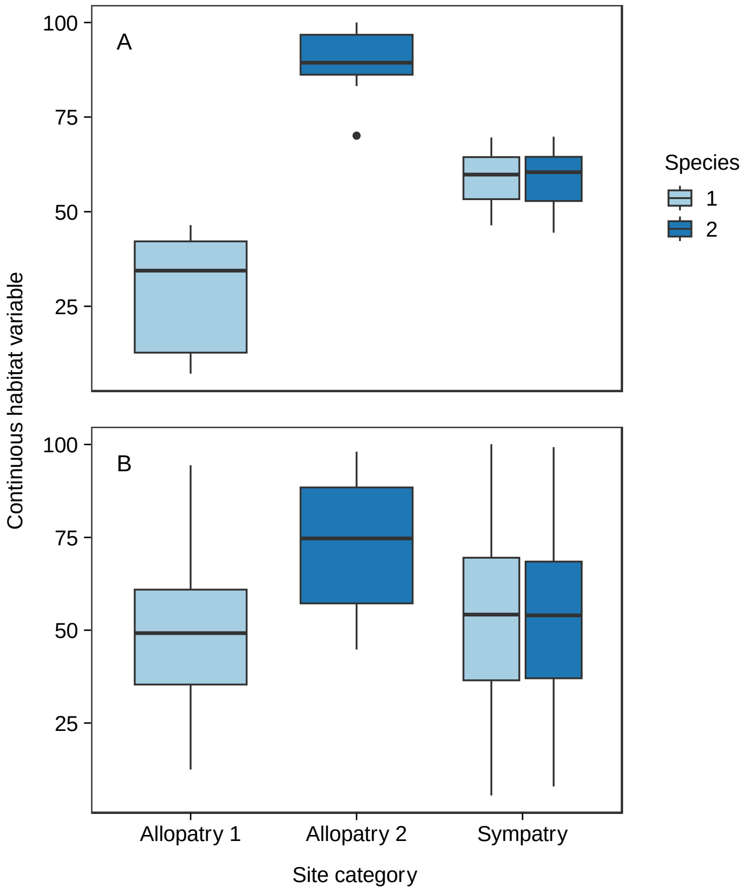

Figure 1. Monte Carlo simulations illustrating that sympatry-allopatry comparisons of habitat use are biased toward finding greater differences in allopatry than sympatry. Two extreme situations were modeled. (A) Linear habitat gradient with areas of allopatry around a contact zone in intermediate habitat. In this simulation, sites were assigned to allopatry-sympatry categories so as to mimic the common situation in which species ranges overlap in transitional habitat. (B) Irregular habitat gradient or mosaic with no correlation between species and habitat. In this simulation, sites were assigned to allopatry-sympatry categories at random to mimic a situation in which species ranges are independent of habitat. In both simulations, 200 individuals settled at random into different cells (representing territories) at each of 30 sites. The sites varied in the mean of a continuous habitat variable (site means were randomly drawn from a uniform distribution with values ranging from 5 to 100); within sites, habitat heterogeneity was normally

distributed around the site mean with a standard deviation of 10 (to represent within-site variation in habitat among territories). Prior to settlement, sites were sorted from low to high mean values of the habitat variable for simulation A and left unsorted for simulation B. After settlement, the first 10 sites had only species 1 (Allopatry 1), the next 10 sites had both species in equal proportions (Sympatry), and the last ten sites only had species 2 (Allopatry 2). The same simulated dataset was used for both simulations; only the order of the sites, and hence the sympatry-allopatry categories assigned to the sites, differed. Boxplots depict the median (horizontal line within the box), interquartile range (box), and lower and upper adjacent values (whiskers). Simulations were run in R version 4.2.2 (The R Foundation for Statistical Computing). The simulation code is available for download (see Data and Code Accessibility).

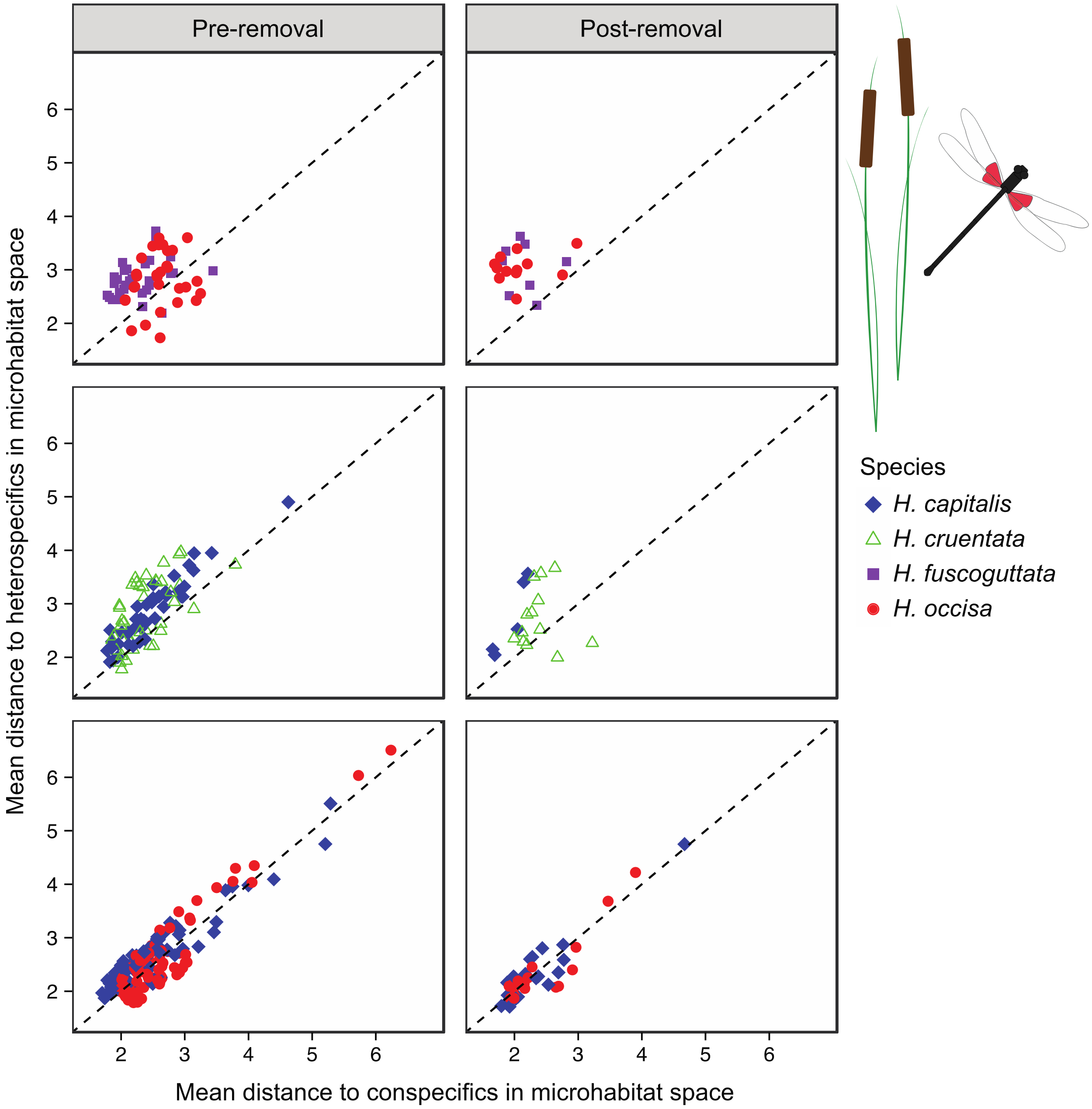

Figure 2. Distances between conspecific and heterospecific territory holders in microhabitat space at each of three sites, before and after experimental removals. Each row of panels represents a different site. Each point represents one territory holder's mean distance to conspecific and heterospecific territory holders. Dashed lines indicate equal distances to conspecific and heterospecific territory holders. Points above the dashed lines are cases in which

the male’s mean distance to heterospecific territory holders was greater than his mean distance to conspecific territory holders. Thus, a preponderance of points above the dashed line indicates that the species differ in microhabitat (for statistical tests, see Table 2). Only territories in removal sections are included in the post-removal panels. For information about the study sites, see Table 1. Sites are in the same vertical order in all figures and tables.

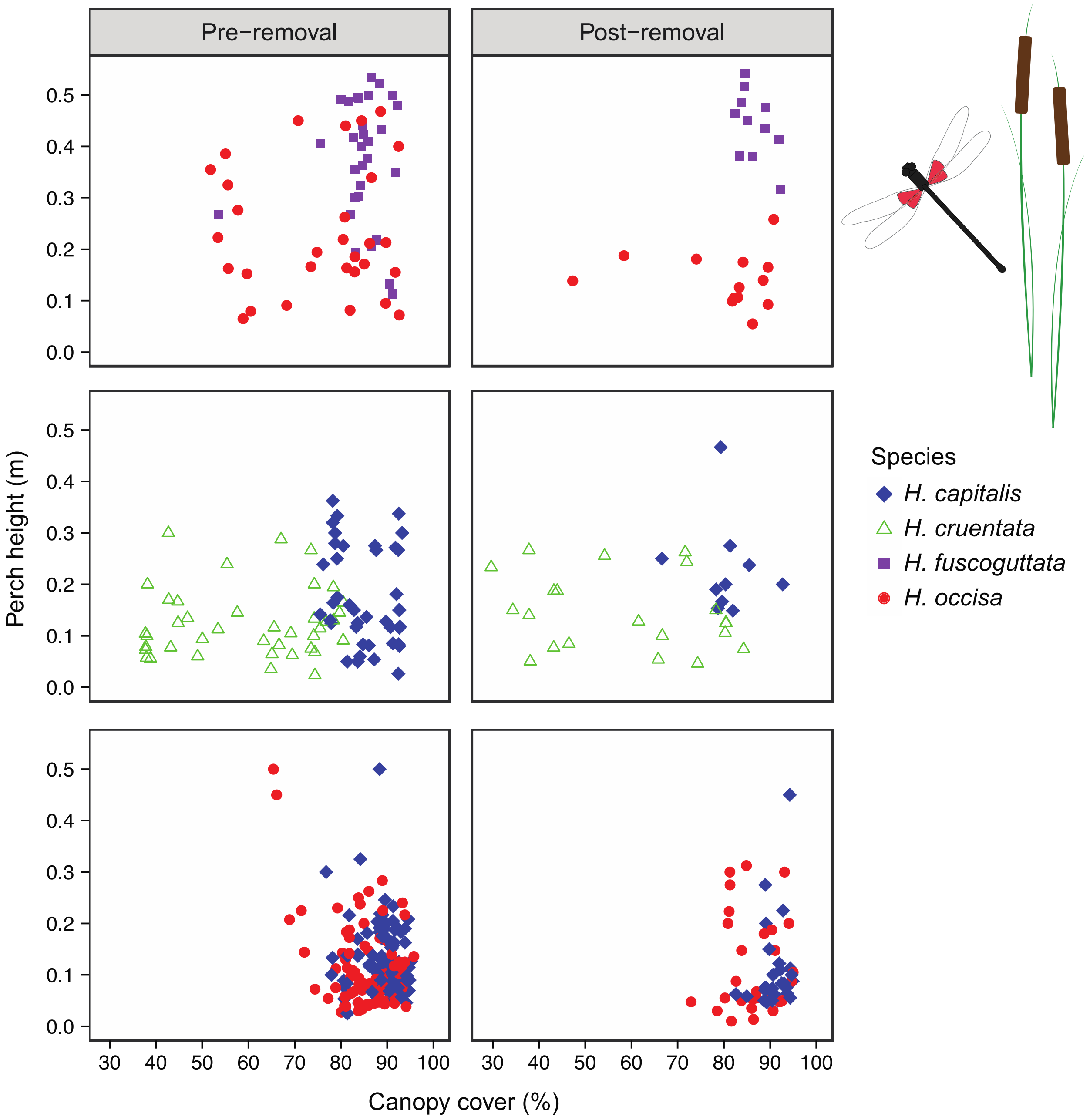

Figure 3. Scatterplots showing variation in territory microhabitat of two species at each of three sites, before and after experimental removals. Each row of panels represents a different site. Each point represents one territory holder's mean perch height and the mean canopy cover on his territory. Only territories in removal sections are included in the post-removal panels. For

scatterplots of the other two microhabitat variables, see Figure S2. For information about the study sites, see Table 1. Sites are in the same vertical order in all figures and tables.

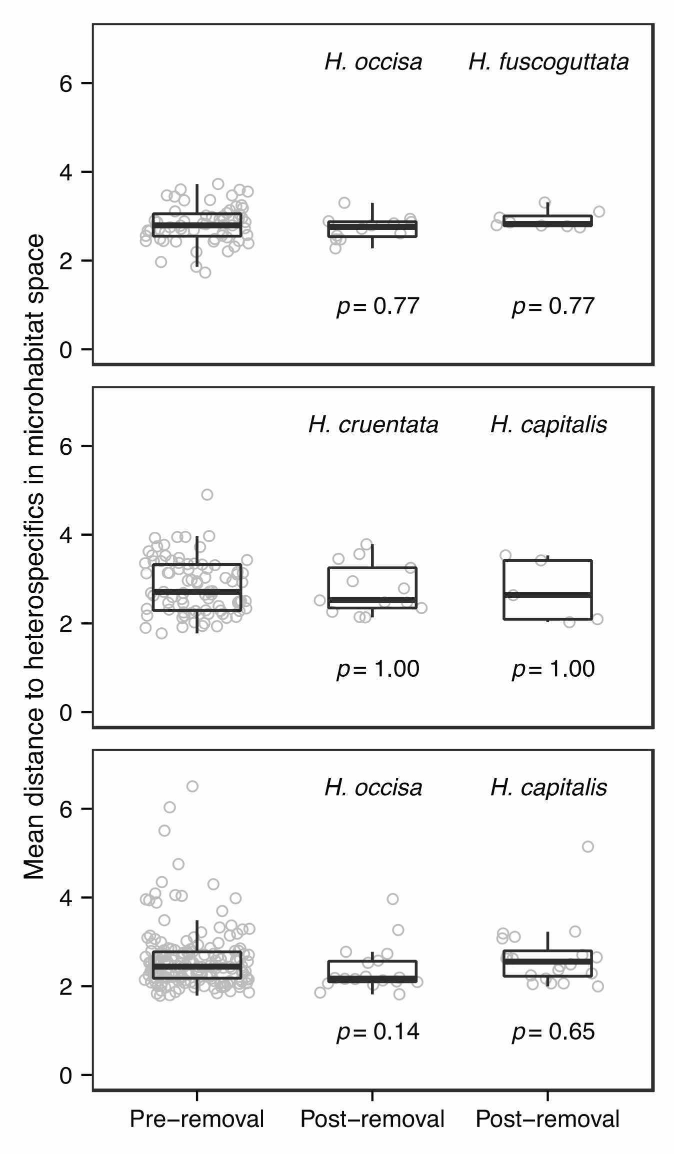

Figure 4. Boxplots illustrating that none of the species shifted toward the other species' microhabitat after the experimental removals. Each panel represents a different site. Each point (gray circle) represents one territory holder's mean distance in microhabitat space to territory holders of the other species that were present before the experimental removals. The pre-removal groups include all territory holders that were present before the removals. The post-removal groups only include males that established territories in removal sections after the removals. Wilcoxon tests were used to compare post-removal groups to pre-removal groups. The *p*-values

were corrected for multiple tests (within sites) using Holm’s method. Boxplots depict the median (horizontal line within the box), interquartile range (box), and lower and upper adjacent values (whiskers). Points were jittered horizontally to reduce overlap. Sites are in the same vertical order in all figures and tables.

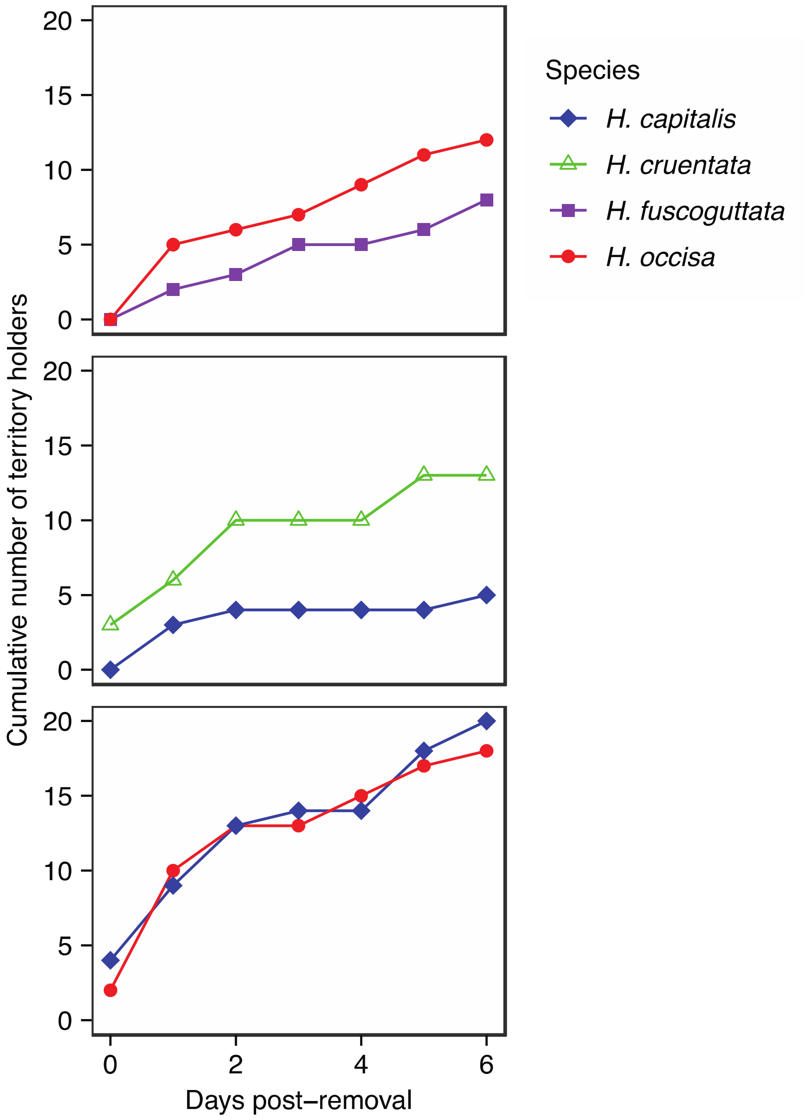

Figure S1. Post-removal territory settlement. Each panel represents a different site. Each point represents the cumulative number of new territory holders of each species on each day following experimental removals at three sites. Only territories in removal sections are included. For information about the study sites, see Table 1. Sites are in the same vertical order in all figures and tables.

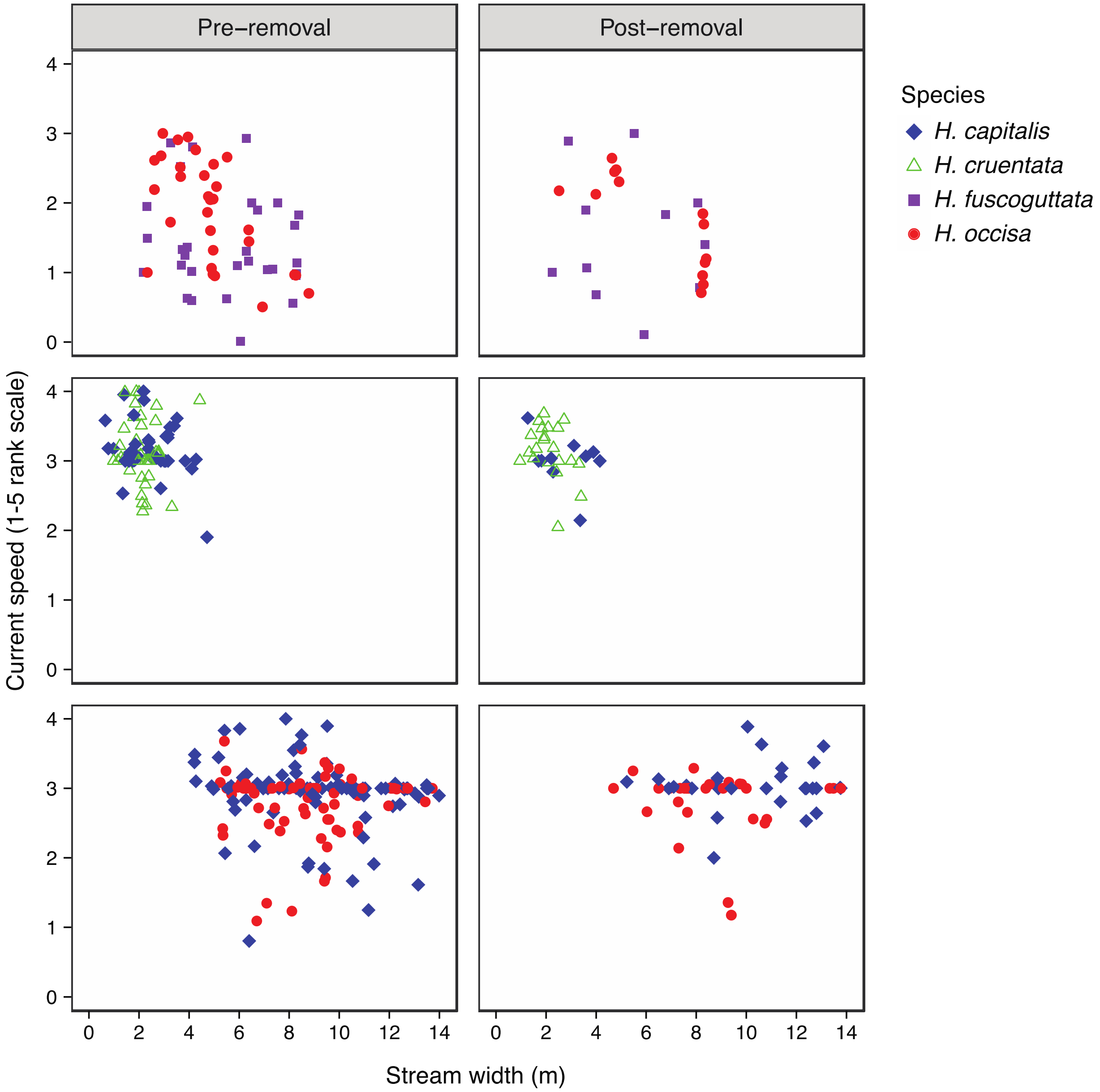

Figure S2. Variation in territory microhabitat of two species at each of three sites, before and after experimental removals. Each row of panels represents a different site. Each point represents the mean current speed and stream width on one male's territory. Only territories in removal sections are included in the post removal panels. For information about the study sites, see Table 1. Sites are in the same vertical order in all figures and tables.

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