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The mosaic effect: habitat fragmentation and microhabitat partitioning among three wren species in San Luis, Costa Rica

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ABSTRACT

Increasing human presence in previously forested areas leads to the alteration and fragmentation of habitats used by resident species of birds. In this study I examine the effects of a mosaic-like arrangement of habitat types on the abundances and distributions of three species of wrens, the House Wren (*Troglodytes aedon*), Plain Wren (*Thryothorus modestus*), and Rufous-and-white Wren (*Thryothorus rufalbus*) to determine any resulting differences in abundances and distributions between species. I conducted visual and auditory observations of wrens during timed walks through four habitat types in the San Luis valley of Costa Rica including primary forest, secondary forest, disturbed home and garden areas, and cleared pastures. Wrens were observed to partially overlap in range likely due to factors of proximity and niche partitioning on the basis of overall habitat, microhabitat, and edge characteristics, but not tree height. Overall wren abundance was equal between species but differed between habitats, and abundance was higher in disturbed areas with high heterogeneity than in homogeneous disturbed areas. Effects of human disturbance are thus demonstrated to vary based on structural characteristics in terms of species response.

INTRODUCTION

Worldwide problems of habitat loss and fragmentation are currently posing increasing pressures on biodiversity and species distributions. Human presence in and use of land causes alteration of natural community structures, as exemplified by processes of deforestation and land transformation for homes and agricultural purposes. Because species rely on particular habitat characteristics to which they are adapted, changes in natural environments can be disastrous for survival (Barbosa *et al.*, 2010). Examinations of disturbances have often confirmed such reductions in resident avian diversity and abundance (Lee *et al.*, 2010), indicating threats to future biodiversity associated with continued development. However, species can respond differently to similar pressures (Wilson *et al.*, 2009).

The valley of San Luis, Puntarenaes, Costa Rica presents a unique and interesting place in which to study habitat fragmentation, being characterized by a mosaic-like mix of areas of varying disturbance levels. Intact primary forest exists alongside areas of secondary growth near rivers and human disturbance, interspersed with farms, gardens, and pastures and divided by dirt roads. This arrangement creates both areas of isolation and corridors for movement among overall fragmentation, all within close proximity. “Edge” areas are common at habitat interfaces and create differences in conditions such as light penetration and soil moisture (Kupfer & Runkle 2003, Chazdon & Fetcher 1984). I chose to examine the distribution of wrens within such an

environment due to their highly vocal and visible nature as well as the high dispersal abilities of birds. For these reasons as well as their differences in preferred habitat, I expect wrens to provide a strong indicator of the effects of fragmentation on species interactions including microhabitat selection and niche partitioning in cases of non-analog community formation.

Previous studies in the Puntarenas region have examined wren distributions based on elevation gradients and microhabitat differences, as well as overall bird diversity as a function of disturbance. Niche partitioning among wrens was determined to occur between both foraging height in trees (Cronholm 1999) and varying forest disturbance levels (Burke 2004). In this study I extend the reach of these findings to include higher levels of human disturbance and occupation including home and garden areas as well as cleared pastures, using a local subset of wren species consisting of the House Wren (*Troglodytes aedon*), Plain Wren (*Thryothorus modestus*), and Rufous-and-white Wren (*Thryothorus rufalbus*).

Due to the close proximity of the habitats in focus, I hypothesize that wrens will occur in areas outside their expected ranges and therefore experience overlap. I aim to determine whether such shifts and coexistence occur, and if so, whether wrens respond via niche partitioning or competitive exclusion. I will then explore potential implications of wren habitat preferences in the context of a changing landscape to make predictions regarding future populations.

METHODS

Study Sites

I determined four habitat types for comparison within the San Luis Valley, all within the Holdridge Life Zone of premontane moist forest between elevations of 1000 and 1200 meters. Habitat A = Homes and gardens, characterized by high heterogeneity of microhabitat including domestic structures, cleared lawns and small fields, mixed trees and crops, integrated forest edge, and gardens of both native and exotic flora. Habitat B = Primary forest, characterized by old growth and closed canopy with low light penetration, lacking human disturbance. Habitat C = Secondary forest, having undergone disturbance and subsequent recovery or occurring along primary forest edges; characterized by lack of a closed canopy cover, higher levels of undergrowth, and younger flora including more pioneer and light-loving species. Habitat D = Pastures, characterized by open grassy expanse and minimal tree occurrence. The only instances of continuous tree cover in pastures were located in dividing lines or segments one or two trees thick.

Study Organisms

The House Wren, Plain Wren, and Rufous-and-white Wren are all insectivorous members of the Troglodytidae family known to occur in the Puntarenas region of Costa Rica. The known preferred habitat types of the three species differ, however. The House Wren probably once preferred scrubby second growth areas and riversides, but has adapted its range to human habitats such as yards, doorways, and roofs, where they commonly nest. The Plain Wren is known to occupy areas of dense second growth or overgrown field areas but to avoid closed tree cover. The Rufous-and-white Wren prefers moist forest habitat in dry areas but adjusts to more open habitats in wetter areas (Stiles and Skutch 1989).

Sampling Design

I located four trails of approximately one hour's walking distance in each habitat type. I visited one trail each at two sites per day for a total of eight days, alternating the hour of visitation so as to correct for potential variances due to time of observation. Sites were either visited early (between 06:30 and 08:30 GMT) or late morning (between 08:30 and 10:30 GMT). I conducted both visual and auditory observations of wrens, documenting species name, microhabitat type, height, and presence of habitat edge characteristics. Microhabitat types were divided into five categories as follows: Microhabitat A = Clustered trees bordering open space, where open space is defined as cleared road, pasture, or lawn without tree cover, and is adjacent to two or more sides of the tree area. Microhabitat B = Forest border, composed of closed tree canopy, at the edges of open or mixed microhabitats. Microhabitat C = Single tree, standing within open space such as pasture or lawn and disconnected from other trees or tree cover. Microhabitat D = Mixed native trees among crops, including coffee, bananas, and varieties of citrus. Microhabitat E = Ground, shrubs, and fences up to 1 meter in height. Height of observation was estimated visually, and mean height values were calculated for individuals that varied position during observation.

To determine whether wrens spatially partition between microhabitats based on edge characteristics, I focused on primary and secondary forests as well as pastures, where edges were most defined. Home and garden habitat was not considered due to its high intrinsic heterogeneity and lack of distinct edges. Edges within focal habitats were defined as areas within 10 meters of a different bordering habitat type.

RESULTS

I recorded a total of 168 observations of wrens among the four distinguished habitat types. Due to the territoriality of wrens I assume that observations are generally of distinct individuals, although due to the proximity of some sites visited, slight overlap may have occurred. Although I observed no difference in overall abundance between the three different species of wren ($X^2 = 0.036$, d.f. = 2, $p > 0.05$), there were significant differences in wren abundances ($X^2 = 29.2$, d.f. = 3, $p < 0.05$) and species distributions ($X^2 = 42.07$, d.f. = 6, $p < 0.05$) between habitats (Fig. 1). House Wrens occurred most often in home and garden areas as well as in pastures, while occurring less than expected in forested areas. Only one House Wren was observed in a primary forest habitat, and the individual was considered to be in forest edge space. Plain Wren individuals were observed across all habitats, but showed higher abundance in secondary forest. Rufous-and-white Wren distribution was concentrated in both primary and secondary forests, showing apparent dominance in primary forest with respect to other wren abundance. Total wren abundance was highest in mixed home and garden habitat and lowest in pastures (Fig. 1).

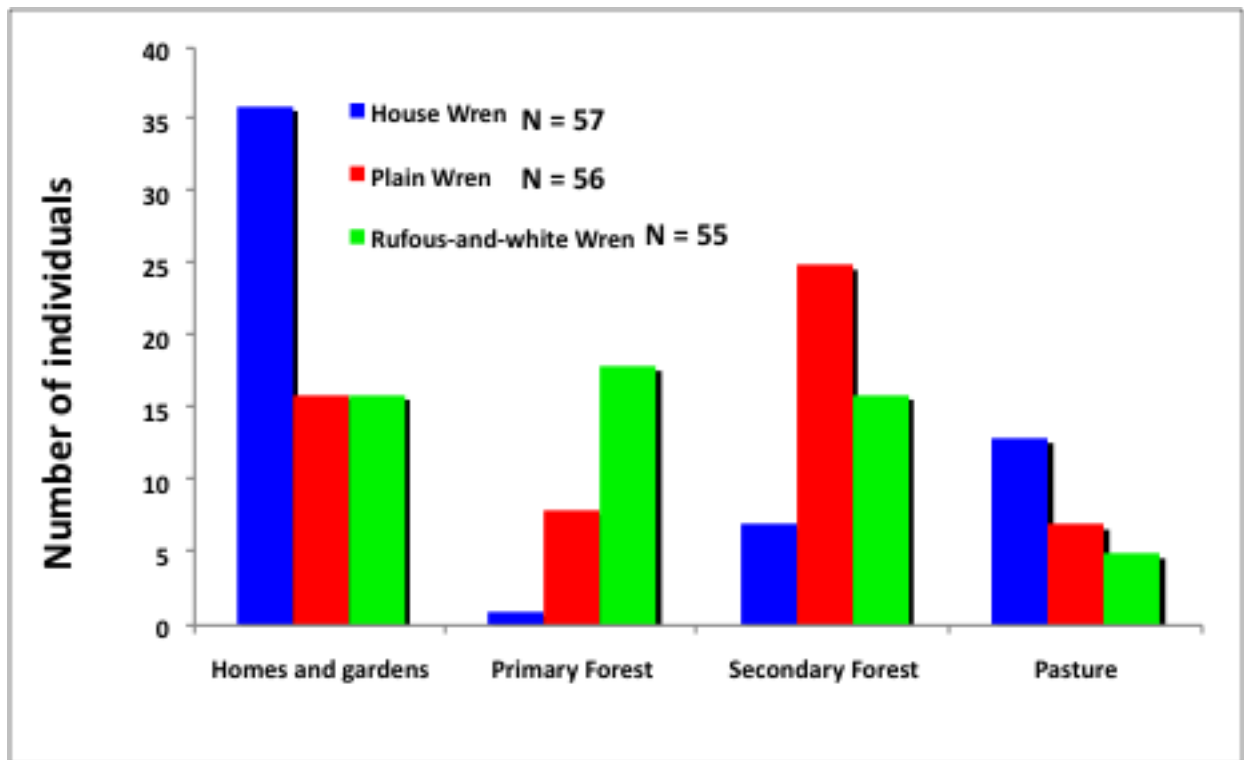


Figure 1: Abundances of three wren species among four habitat types in close proximity within a premontane moist forest zone. Significant differences in species distributions were observed ($X^2 = 29.2$, d.f. = 3, $p < 0.05$).

The habitat displaying the greatest number of wrens in overlap was mixed homes and gardens. Within this area mean tree height at which observed individuals occurred does not reveal any significant difference between species (ANOVA: $F_{(2,65)} = 2.94$, $p > 0.05$; Fig. 2). However, distribution between microhabitats defined by tree type and cover exposes significant trends ($G = 25.74$, d.f. = 2, $p < 0.05$). The distribution of House Wrens includes ground and areas below 1 meter, whereas no other wrens were observed in this space. Similarly, Plain Wrens were found in mixed crop trees, where no other wrens occurred. Rufous-and-white Wrens occurred exclusively within tree cover, both bordering open space and within closed forest borders. However, both House Wrens and Plain Wrens were also seen occurring in these spaces. House Wrens constituted most observations of birds seen in single trees, although Plain Wrens were also occasionally noted there (Fig. 3). There were also significant differences in occupation of edge space between wren species ($G = 21.21$, d.f. = 2, $p < 0.05$; Fig. 4).

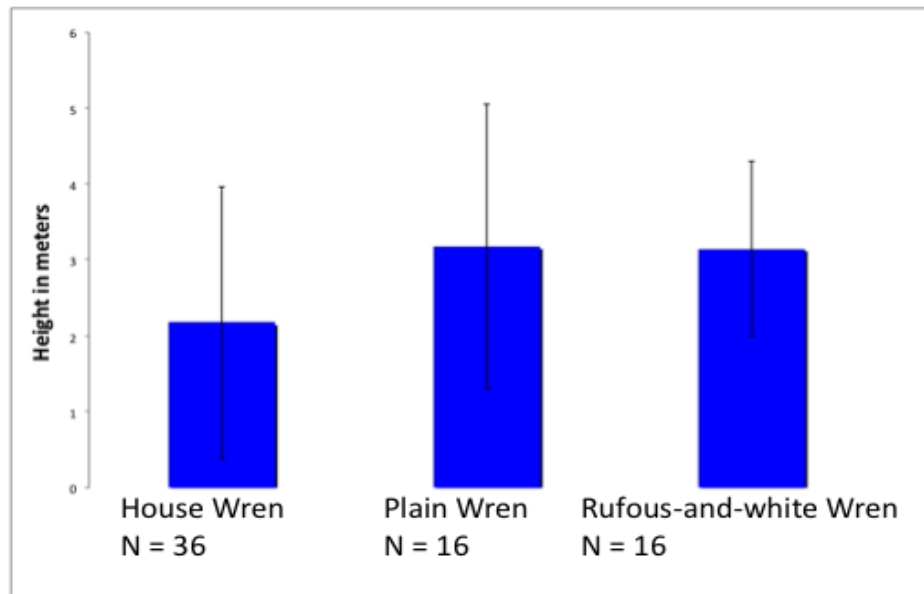


Figure 2: Distribution of tree-height-based observations of three wren species in a heterogeneous disturbed habitat of homes and gardens. No significant difference was found (ANOVA: $F_{(2,65)} = 2.94$, $p > 0.05$). House Wren height mean = 2.18 ± 1.79 , Plain Wren height mean = 3.19 ± 1.87 , Rufous-and-white Wren height mean = 3.16 ± 1.15 .

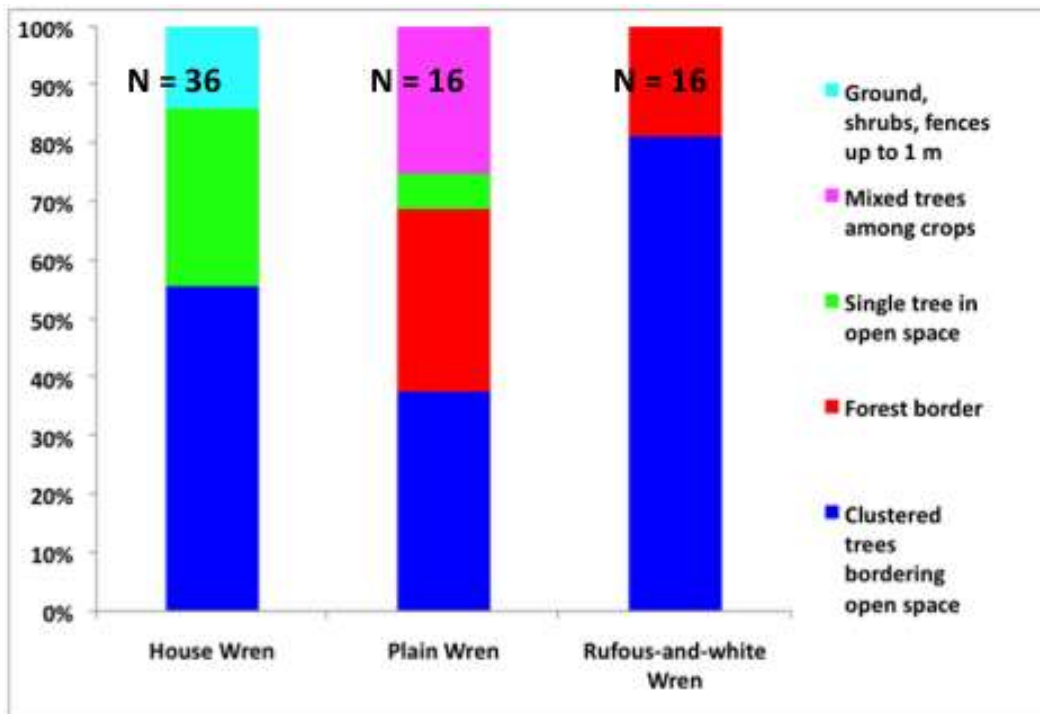


Figure 3: Percentage distributions of three wren species into microhabitat types. Observations were taken within a heterogeneous disturbed habitat of homes and gardens. Significant niche partitioning was observed ($G = 25.74$, $d.f. = 2$, $p < 0.05$).

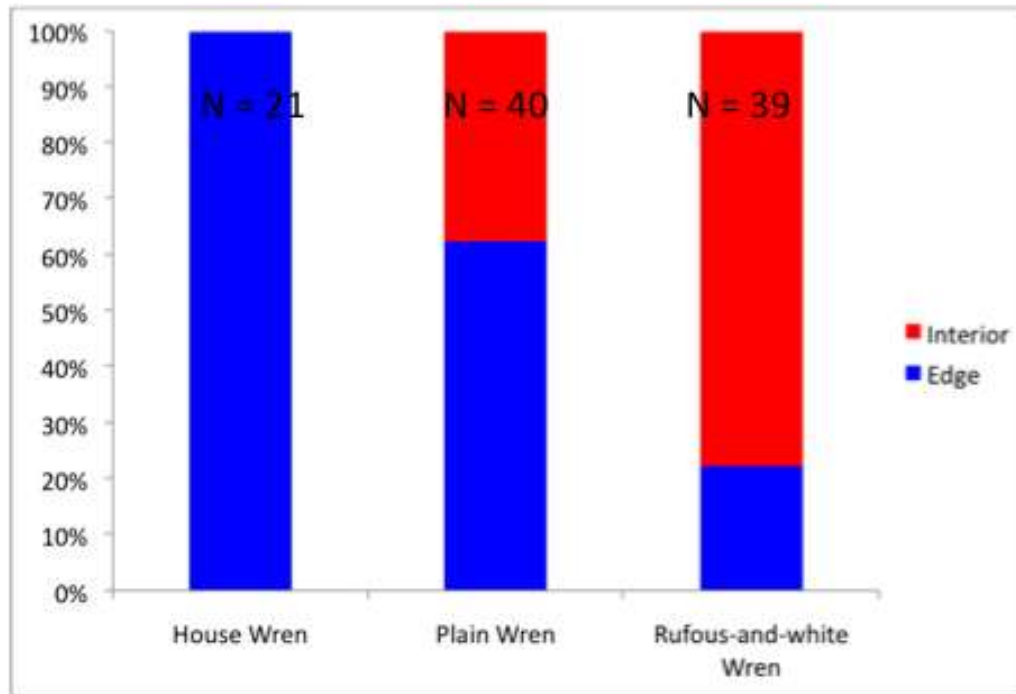


Figure 4: Percentage distributions of three wren species into edge and interior habitat. Observations taken within primary and secondary forest as well as pastures, and edges defined as space within ten meters of different adjacent habitat. Significant differences in edge usage between species were observed ($G = 21.21$, $d.f. = 2$, $p < 0.05$).

DISCUSSION

According to the distribution observed in this study, wrens do overlap throughout differing habitats of close proximity, but significant trends in abundance and diversity occur both between and within habitats. The difference in wren distribution between undisturbed forest and disturbed habitats means that either overall wren community composition within the San Luis valley must accordingly change with increasing disturbance area, or otherwise wrens must experience crowding within remaining intact and otherwise suitable habitat. The observation of wrens outside their expected ranges indicates either that individuals are foraging in suboptimal habitats (Winker *et al.*, 1995) or that the new ranges do not constitute a decrease in suitability. Interestingly, the lack of difference in overall abundance between wren species indicates two possibilities.

The first possibility is that no difference in fitness exists between species, and competitive exclusion is not occurring. The wrens must therefore successfully undergo some form of niche partitioning (Hutchinson 1991). My study at least partially confirmed this possibility. Although each wren species displayed significant overall preferences, each was also observed throughout all habitat types. The observation of significant microhabitat partitioning between wrens within a highly heterogeneous habitat indicates that wrens have adapted methods for coexistence. This apparent ability to maintain fitness despite habitat alteration may be

explained by wrens selecting habitat based on highly localized characteristics such as branch configuration rather than larger-scale community or ecosystem types (Hutto 1985). Although tree height in isolation was not in this case an important determinant of wren distribution, amount and type of tree cover did appear to have significant effect. For example, the selection of local areas of tree cover within the greater context of a disturbed area by Rufous-and-white Wrens might mimic conditions within intact forest tree cover and therefore provide just as optimal of an environment.

An apparent problem with this interpretation of the observed wren distribution remains in the level of habitat and microhabitat distribution overlap that still occurs. Rufous-and-white wrens do not occupy any space without House and Plain Wrens. In light of my observation that all wrens appear to be competing and surviving equally, I explain this apparent contradiction with the Theory of Competitive Exclusion (Gause & Witt 1935) by the partitioning of habitats into edge and interior areas. Because edge areas provide different characteristics than forest interiors such as higher light and wind inputs, (Barbosa *et al.*, 2010), certain species have adapted characteristics to take advantage of these additional niches (Hutto 1985). While Plain Wrens were observed within primary forest, which tended to be generally dominated and preferred by Rufous-and-white Wrens, the occurrence of Plain Wrens was largely restricted to edge areas, whereas Rufous-and-white Wrens made greater use of interior space. The proximity of preferred habitats to suboptimal ones may also allow optimal areas to act as source pools for the local movement of species between habitat types (Winker *et al.*, 1995). Interestingly, the observed preference of the Rufous-and-white Wren for closed primary forest corresponds to the species' recorded range within dryer areas, in contrast to its described tendency to occupy more open areas in wetter habitats (Stiles and Skutch 1989, Burke 2004). Its increased presence in wet primary forest may therefore represent a shift into suboptimal habitat caused by competition with the Plain Wren for secondary-like growth (Winker *et al.*, 1995).

The second possibility for explaining the lack of difference observed between wren abundances is that the apparent equilibrium may in fact reflect not coexistence but a rather an isolated time state within an ongoing process of competition and eventual exclusion (Sirami *et al.*, 2009). Further examination of this system over longer time scales is needed to determine whether local wren populations are actually in equilibrium or undergoing change. If habitat transformation continues favoring certain habitat types, the abundance proportions of wrens may shift toward the proportion observed in that habitat; because House Wrens were observed to succeed within disturbed habitat, their population in San Luis is likely to grow with increasing disturbance. Furthermore, mosaic-like division of environments increases the proportion of edge space within habitats, which can alter species compositions by changing characteristics and suitability (Kupfer and Runkle 2003). In this study, Plain Wrens appear to benefit by the creation of more edge space.

An examination of overall abundance reveals that while areas of disturbance contain different amounts of overall wren presence than forested areas, this effect is dependent on the type of disturbance. In terms of the species considered here, abundance of individuals actually increases in all home and garden areas in comparison with primary forest, for example, while remaining relatively unchanged in pastures (although examination of pasture interiors or pastures without edge trees would likely return lower wren abundance, according to trends observed in this study). Observations of increased bird abundance in disturbed areas may appear to contradict findings of numerous other studies (Lee *et al.*, 2010). However, my study does show a shift in species success and dominance occurring in both types of disturbed habitat, with the House

Wren benefiting. This result agrees with previous studies' findings of shifts in community composition toward different or more generalized species in the presence of disturbance (Sirami *et al.*, 2009). Furthermore, overall wren responses to disturbance appear to depend on the heterogeneity of the resulting habitat. Each habitat observed in this study is comprised of a combination of the microhabitats also described. When viewed as such, the abundance of wrens within a habitat becomes a function of the amount of microhabitats or niches available. Therefore structurally heterogeneous disturbed habitats such as homes and gardens may be much less detrimental to sustaining populations than homogeneous disturbances such as pastures.

Despite this observation, the restricted variety of species considered in this study necessitates the consideration that all organisms do not respond similarly to such factors. Nonmigrant species, for example, may select habitat based on differently scaled characteristics than migratory species or species with wider day-to-day ranges (Hutto 1985) and thus microhabitat partitioning may not be possible for other species, resulting in their exclusion from disturbed habitats. Such complex potential trends are important to consider and study further in the face of further development due to their implications for future biodiversity.

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