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Bowerbird species are divergent in bower canopy structure, hence display lighting

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ABSTRACT

Male Bowerbirds (Ptilonorhynchidae) build bowers, which are only used for attracting and mating with females. All bowers are built under a vegetation canopy, but canopy structure appears to vary among species. Canopy structure affects light quality and mating display visual contrast, hence it is worth investigating. Hemispherical camera photography was used to record canopy structure over active bowers, abandoned bowers and control sites for 7 Australian species. Different species showed significantly different patterns of canopy gaps, and sympatric species were more different than allopatric species. The differences between active, abandoned and control sites in the same vegetation strongly suggest active and continuous microhabitat choice. Differences among sympatric and allopatric rainforest species suggest a character displacement pattern. The results suggest that the vegetation geometry can affect where a species chooses to live and reproduce, and could apply to other species.

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Introduction

An important part of survival and reproduction is choosing the appropriate habitat and microhabitat because it provides accessible and predictable conditions for life (Cody 1985). For example, Marshall *et al.* (2016) found that island lizards choose microhabitats that enhance crypsis, and the effect is smaller in islands with lower predation intensity. In a large phylogenetically controlled study of thousands of bird species, Dunning *et al.* (2025) found a significant association between plumage colours and habitats, which could be a secondary result of plumage-based natural selection for anti-predation and within-species communication under specific light conditions. Microhabitat choice is not simple because it involves very different kinds of choices and has to be simultaneously optimised for foraging, attracting mates, reproduction, and escaping predators.

Microhabitat choice is hard to study because it is difficult to define and recognise critical microhabitat properties that are used as cues in choice. Some success has been achieved by careful descriptions of vegetation structure and composition, for example in Birds (Martin 1998; Li *et al.* 2020) and reptiles (Marshall *et al.* 2016; Mizsei *et al.* 2024). More precise descriptions of microhabitats can be obtained when individuals repeatedly return to the same place within a season, as in some bird nesting sites (Martin 1998) and bowerbird bowers (Frith and Frith 2004).

Bowerbird (Ptilonorhynchidae) males build and decorate a structure (the bower) out of twigs and other objects which is used only for mate attraction and mating (Frith and Frith 2004). Formally, Toothbilled Bowerbirds (*Scenopoeetes dentirostris*) do not have a bower in the sense of a stick structure, they just put a layer of freshly cut leaves of a few species on the forest floor with their white underside facing upwards on the court (Frith and Frith 1994, 2004; Frith 2016). However, this structure or court is just as important in mating location as 'regular' bowers, and other species have both courts and structures so using "court" for all species would be confusing. The leaves are carefully placed and this is 3D, so this is in fact a structure, just much simpler than in other species. Therefore I will refer to the Toothbill court as a 'bower' purely for brevity and uniformity with the other species. Bowerbirds have an additional site location problem because their bower is on the ground, its location is stable for months, it is constantly tended by the male and is physically separate from nesting. This suggests greater predation risk but also makes it practical to identify microhabitats used for courtship and mating. Here, I investigate microhabitat properties for 7 Australian bowerbird species using hemispherical photographs of the canopy over

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bowers. The vegetation canopy affects the quality of light (Endler 1993), which directly affects display efficiency and success and may help both males and females to find the bowers (Endler *et al.* 2014).

Given that most rainforest bowerbird species are sympatric (Pizzey *et al.* 2007) their canopy structures may be different, and perhaps more different than between the two woodland species studied. A pattern consistent with character displacement might occur among bowerbird species if microhabitat choice is used for bower location and if sympatric species show larger differences than allopatric species. This suggestion is about pattern and not process because there are multiple different processes, which can result in a character displacement pattern (Stuart *et al.* 2017). At the very least, woodland species should be more strongly illuminated than rainforest species because woodland canopies are discontinuous. Rainforests have closed canopies, but the degree of closure (the canopy gap distribution) is spatially heterogeneous, so species differences are possible, but it is impractical to make predictions about rainforest canopy structure consequences without direct measurements. Canopy geometry measurements are the main purpose of this study.

Methods

Species and study area

Bowers were found, and canopies above them were photographed with a hemispherical lens and camera. This was done in the geographic ranges of 7 bowerbird species: Great (*Chlamydera nuchalis*), Spotted (*Chlamydera maculata*), Fawn-Breasted (*Chlamydera cerviniventris*), Satin (*Ptilonorhynchus violaceus*), Regent (*Sericulus chrysocephalus*), Golden (*Prionodura newtoniana*), and Toothbilled Bowerbirds (*Scenopoeetes dentirostris*) (Note that some authors regard *Chlamydera* as a synonym of *Ptilonorhynchus*, e.g. Christides and Boles 2007). The Great and Spotted bowerbirds are found in woodland (trees with discontinuous canopy and many open areas) and the other 5 species are found in rainforest (continuous forest canopy), see Frith and Frith (2004) and Pizzey *et al.* (2007). The two woodland species are allopatric (not found together in the same place) except for a narrow hybrid zone in central Queensland (Frith *et al.* 1995). Except for the Fawn-Breasted Bowerbird, which is allopatric with the others, the other rainforest species are sympatric, and their bowers can be found within tens of metres of each other (personal observations 1996 to 2024; also known as microsympatric).

Active bowers were sampled and defined as active by the presence of an intact, well-constructed bower (Frith and Frith 2004) and fresh decorations (fruits, flowers, insects, snake skins, lichens, leaves and artificial objects such as glass, plastics, and metals). Abandoned bowers were found and sampled nearby. They were identified by partially or wholly broken down bowers and fewer ornaments than the active bowers. Because Regent Bowerbird bowers are difficult to find, I could not find their abandoned bowers. Because Toothbilled Bowerbird bowers (courts) are made of ephemeral leaves, finding abandoned bowers is essentially impossible. Bowers of young males are often smaller with somewhat fewer ornaments but still have a normal (if smaller) shape and ornaments (distribution clearly discontinuous), consequently, they were not included in the analysis. In addition, photographs were taken nearby under the same vegetation as the active bowers, these are referred to as controls. A direction and distance were chosen at random as the control. However, both Great and Spotted Bowerbird bowers are almost always placed under shrubs (mostly in the genus *Carissa*) with an emergent tree above them, so controls were located under similar-shaped shrubs of the same species as over the closest active bower. They are microhabitat controls rather than habitat controls.

Sample sizes of Great Bowerbird active bowers, abandoned bowers, and control sites were 714, 97, and 132, respectively. Bowers were found in 23 localities across the entire geographic range of Great Bowerbirds (Figure S1). Of these, 8 had buildings or other human disturbance, consequently, in the interests of getting natural habitat structure, these were not used in this study. These localities span both the western and eastern subspecies (*Chlamydera nuchalis nuchalis* and *C. n. orientalis*); the subspecies are roughly split by the Gulf of Carpenteria (Frith and Frith 1999).

Bowers of other species were sampled from fewer localities and bowers, sample sizes were: Spotted (116, 52, 44, Taunton National Park QLD), Fawn-Breasted (6, 3, 29, Iron Range QLD), Regent (8, 0, 27, O'Reillys, Lamington National Park, QLD), Satin (25, 11, 27, Atherton region, Paluma, Bunya Mts, O'Reillys, Lamington National Park QLD), Golden (28, 5, 20, Atherton region and Paluma, QLD), and Toothbill (33, 0, 21, Atherton region and Paluma QLD).

Data collection

At each bower, a 360° solid angle hemispherical ('fisheye') photograph was taken to capture the canopy structure (Figure 1(A)). Photographs were also taken at abandoned bowers and microhabitat control (no-bower) sites under the same vegetation. Hemispherical photographs are a useful way of estimating canopy cover in relation to microhabitat choice and behaviour (examples in

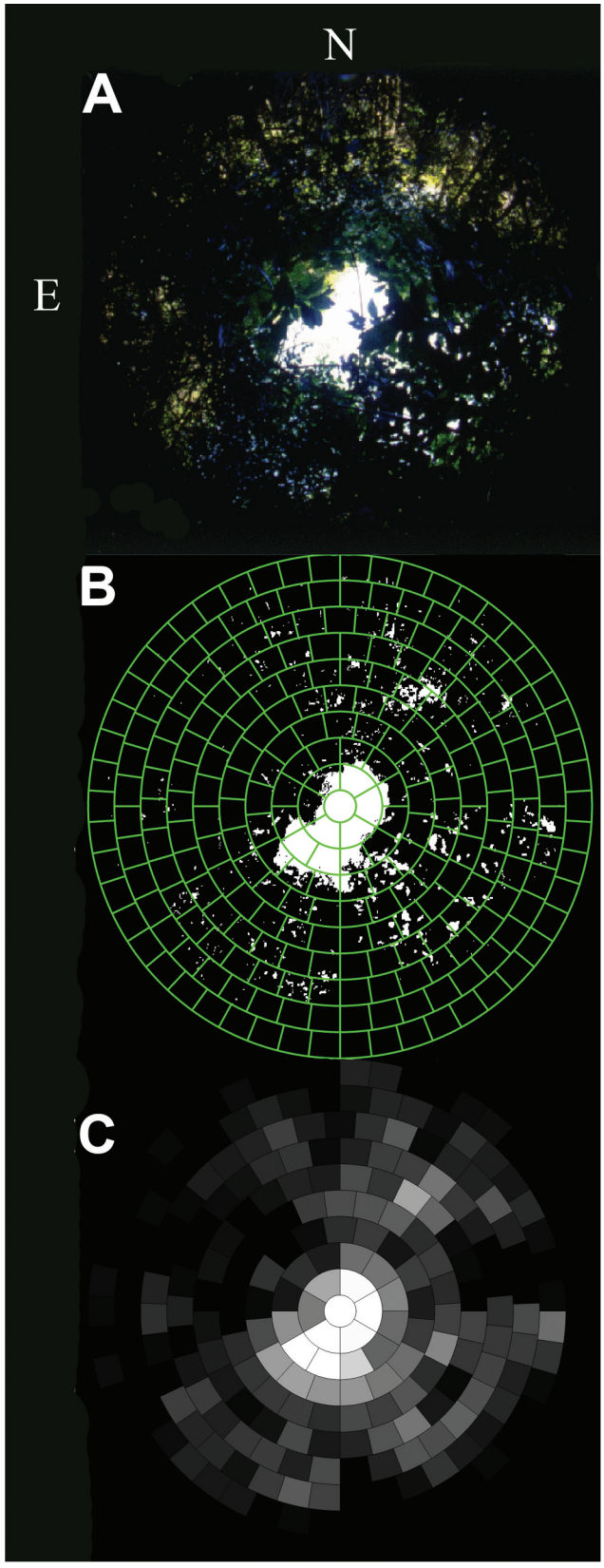

Figure 1. Analysis of a hemispherical photograph. A: Original hemispherical photograph of canopy above a satin Bowerbird bower court. B. Blue channel thresholded image with a superimposed grid of sectors. C. Gap fractions in each sector with white being 100% gap (all sky showing) in that sector and black being 0% gap (no sky showing). N and E are cardinal directions; E is left because the camera is facing upwards.

Giannetti *et al.* 2024; Backhouse *et al.* 2025). Here, I look at both overall canopy closure (gap fraction) as they did, but also the geometry of the canopy structure. Photographs were taken with the fisheye lens facing upward and the levelled camera body resting on a bowerbird court with the top of the image oriented towards magnetic north. The camera field of view incorporated the bower at one edge of the field of view. For species such as the Great and Spotted Bowerbirds, with two courts, both courts were measured and data combined for each bower; in others the only court was measured. The purpose was to capture the essence of the selected canopy over the whole bower, regardless of one or two courts. In some cases, I distinguished between the main and secondary courts to test the idea that the main court was more illuminated; the main court was determined by the court with more ornaments, and in many years of video observations almost all male displays took place on the court with more ornaments, which also usually had more light. The main purpose was to test for differences in the details of canopy structure geometry over each bower, not just overall canopy closure.

In the early part of the study, a Canon T70 film camera with a Canon 75 mm 1:5.6 360° solid angle fisheye lens was used; developed Kodachrome film strips were scanned at 1200dpi as jpg. For the bulk of the study, a Canon EOS5D digital body with a Sigma EXDG 8 mm 1:35 360° solid angle fisheye lens was used. Figure sizes before processing were 1.3 to 2.3 MB.

The blue channel of the coloured images was thresholded in MATLAB to black and white using the imbinarize function with a threshold of 0.6. Thresholding was used to estimate the fraction of sky (blue and white) showing through the canopy; sky was assigned 255 (white in thresholded images, see Figure 1(B)). (Thresholding a greyscale image would mistakenly include illuminated leaves and light bark). A grid with 254 sectors was overlaid on the thresholded canopy image (Figure 1(B)). In each sector, the gap fraction was calculated from the total number of white (sky) pixels in the sector divided by the total number of pixels (white+black) in the sector. Figure 1(C) shows the resulting gap fractions of Figure 1(B) where white is 100% sky and black is no (0%) sky showing through the canopy. The set of gap fractions for a given hemispherical photo was used as a response variable in all subsequent analyses. Because the sectors of the outer rim are mostly distant ground and dense vegetation in the horizontal direction, and not actually local canopy, hence mostly black, they were excluded from further analysis, leaving 204 sectors. The overall gap fraction was also calculated from the total white pixels divided by the total pixels in all sectors and was used for overall comparisons of canopy closure.

Analysis

Calculations were done in MATLAB R2024b (Mathworks 2024), and statistical analysis were done in R 4.4.3 (R Core Team 2025).

Overall gap fractions and hence overall light intensity differences were compared by GLM using overall gap fraction (total white pixels divided by all pixels in the thresholded image) as the dependent variable. For habitat (rainforest or woodland) or species comparisons within habitats, habitat or species was a fixed effect. These tests were simply to determine the overall differences between habitats and species within habitat. R, version 4.4.3 (R Core Team 2025) and R packages *lme4* 1.1–37 (Bates *et al.* 2015) and *lmerTest* 3.1–3 (Kuznetsova *et al.* 2017) were used for this analysis and a sample R code and the raw results are provided in the supplemental material.

To estimate the average canopy geometrical structure of a given species, the gap fractions of each sector were averaged over all bower canopy images at the same orientation (North up). For visualisation, each sector mean was divided by the maximum mean, and the results were plotted where the lightness of the sector is proportional to the mean gap fraction of that sector and species. This was done within species separately for active bowers, abandoned bowers and control sites.

In order to quantify species differences in canopy structure, the standard deviation (SD) and Hill Diversity index (h) of sector gap fractions were calculated within each hemispherical photo (as in Figure 1(C)). The standard deviation of sector gap fractions (SD) was calculated on the actual gap fractions and gives an estimate of canopy spatial variability within a canopy image. The Hill Diversity Index (h) was calculated by first dividing each sector gap fraction in a given image by the sum for all sectors in that image, yielding proportions adding to 1 per image. Then h was calculated from these proportions for that image (for details and formula of h see the online supplement). The Hill diversity index is the reciprocal of the classical Simpson diversity index and yields the equivalent number of equally common gap fractions and is an estimate of the evenness of canopy structure.

Geometrical patterns in the canopy structure can also be assessed by means of a spatial autocorrelation (an excellent discussion is found in Srinivasan *et al.* 1982). This avoids the Fourier transform assumption of sinusoidal components. Autocorrelation diagrams are constructed by calculating the correlation between every pair of points (sector centres) for grouped distances. Plotting spatial autocorrelation vs. distance yields information on the pattern. Random patterns show either a quick initial decline of r (the correlation coefficient)

and distance, or a flat curve. Non-random patterns vary in curve shape. Differences among sets of autocorrelations were tested by means of a GAMM using R 4.4.3 (R Core Team 2025) with packages *mgcv* 1.9–3 (Wood 2011) and *itsadug* 2.4.1 (van Rij *et al.* 2022). The *itsadug* package is explicitly designed to account for autocorrelations among points; other methods assume points are independent (van Rij *et al.* 2022), which would be an invalid assumption. A GAMM analysis fits nonlinear curves to the data (Wood 2011), whereas other methods depend upon linear relationships. The GAMM uses the autocorrelation relationship as the dependent variable, distance and bower or status (active, abandoned or control) as smoothing factors. See the online appendix for an example GAMM R code and its outputs.

Results

The Great and Spotted Bowerbirds live in woodland and the other species in rainforest (Frith and Frith 2004). Figure 2 shows the distribution of overall gap fractions for active bowers of each species and their overall microhabitats (controls). Note that the controls are random samples of locations under vegetation because bowerbirds never build in open areas; controls are for microhabitats, not habitat. Woodlands have significantly more open canopies than rainforests (Figure 1 and Table 1) and consequently have more light on the bowers, hence the striking but expected differences in gap fraction distributions among habitats. There are also differences among species in overall gap fractions within habitats (Table 1) which are greater among woodland species. Differences are smaller among species controls within habitats.

Canopy geometry varies among species as well as among active, abandoned and control (non-bower) sites (Figures 3 and 4, Tables 1 and 2). Great Bowerbird canopies (Figure 3(A)) tend to be more open than Spotted (Figure 3(B)); there are more contiguous light sectors in the figure. Great Bowerbird bowers tend to have more light to the north and east (left in diagrams) and Spotted more from upwards (zenith) and less directional. These patterns decline after bower abandonment (Figure 3). The patterns are much more random and spatially more uniform in the control samples. Both Great (Figure 3(C)) and Spotted Bowerbird (not shown) bowers have more light in their main courts (courts with more decorations); this court has many more decorations and most displays take place there. This suggests that light quality is important in displays and mating (see also Endler *et al.* 2014).

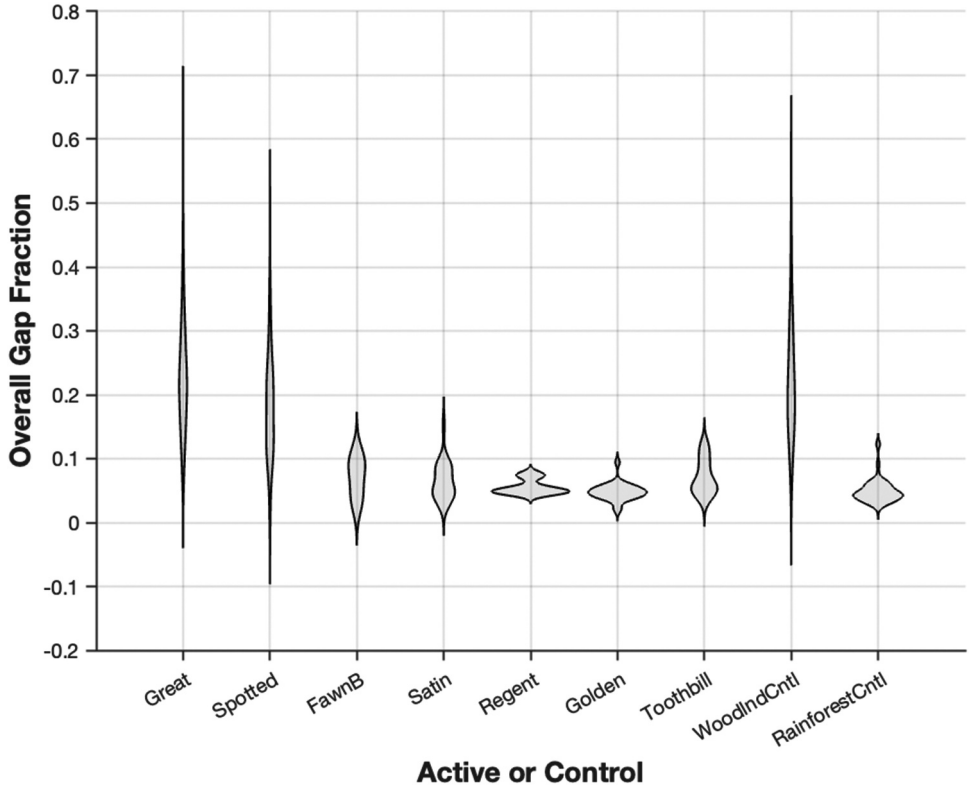

Figure 2. Violin plots of the overall gap fractions for active bowers of each species, and controls pooled by habitat. Values calculated for each image as the number of white pixels divided by the total number of pixels within the hemisphere circle shown in Figure 1B. Table 1 shows statistical tests using GLM among these groups.

Table 1. GLM comparisons of total gap fraction by habitat (fixed factor) & species (random factor). Full statistical test details are in the supplemental material.

Factor	P active	P controls
Woodland vs Rainforest (Habitat fixed)		
Intercept	<2e-16***	<2e-16***
Habitat	<2e-16***	<2e-16***
Differences among species (Species random)		
Woodland Species	2.467e-07***	0.002925**
Rainforest Species	0.00333**	0.003514**

*$p > 0.05$; **$p < 0.01$; ***$p < 0.001$.

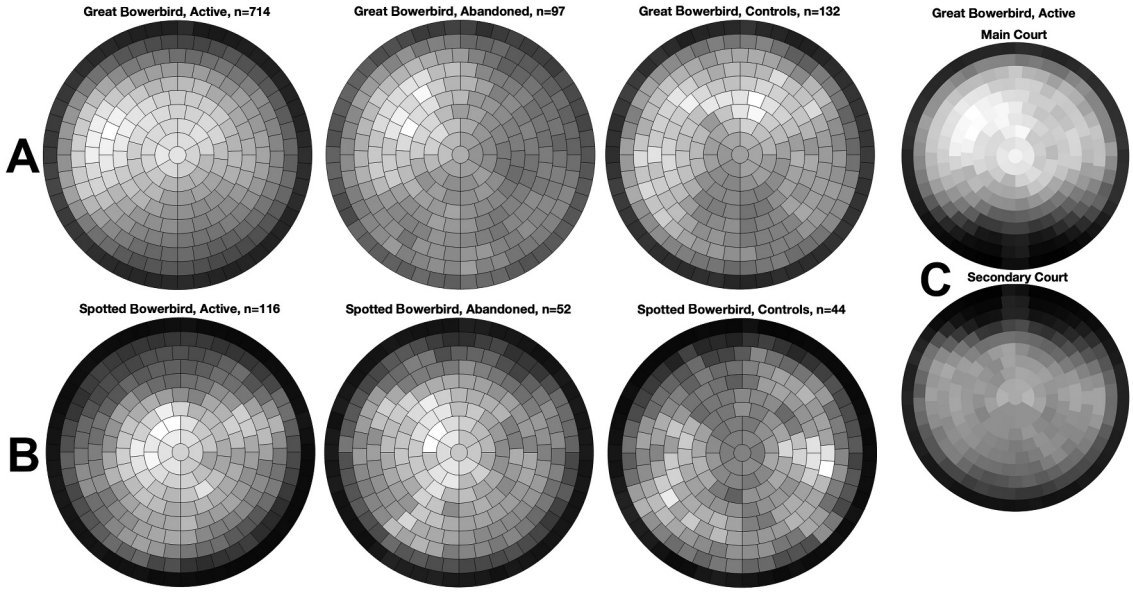

Figure 3. Relative gap fractions for woodland species, Great (A,C) and Spotted (B) Bowerbirds. The first column shows the canopy structure for active bowers, the second for abandoned bowers, and the third for control sites under the same vegetation and shrub species. Figure 3C shows the distribution of canopy gap fractions separately for Great Bowerbird main and secondary courts, regardless of cardinal directions. Main courts have much more decorations, more light, and are the main male display part of the bower. The main point here is the overall gap pattern, not the individual courts.

Control canopy patterns are similar among the rainforest species (Figure 4), but differences among species active bower canopies appear greater than in woodland. Satin Bowerbird bowers have a large canopy gap overhead (Figure 4(A)), and Regent Bowerbird bowers have a weaker gap in the dense vine tangles over their small bowers (Figure 4(B)). Fawn-Breasted Bowerbird bowers have two clusters of canopy holes (Figure 4(C)). Golden and Toothbill bower canopies are more diffuse, with Golden lighter to the south (Figure 4(D)) and Toothbill more diffuse (Figure 4(E)). Abandoned bower canopies are less well defined in the woodland species. Rainforest controls (Figure 4, right column) are diffuse, and not very different from the Toothbill active sites.

Figure 5 shows Hill Diversity h plotted against Gap Fraction SD for all bowers for each species, with convex hulls surrounding data from each species. Fraction overlaps between convex are given in the supplement Table S1. This overlap table shows two values of fraction overlap, one for a given species overlapped by another species and vice versa. The matrix-symmetrical numbers (i, j vs j,i) are different when the relative areas of the two sets of points are different. The two closely related woodland species overlap extensively (61% and 97%), with Great Bowerbird gap fraction sector diversity ranging higher than Spotted bowerbirds (Figure 5(A)). The pattern of overlap in the rainforest species (Figure 5(B)) is interesting because the sympatric species (Satin, and Regent in the south, Satin, Golden and Toothbill in the

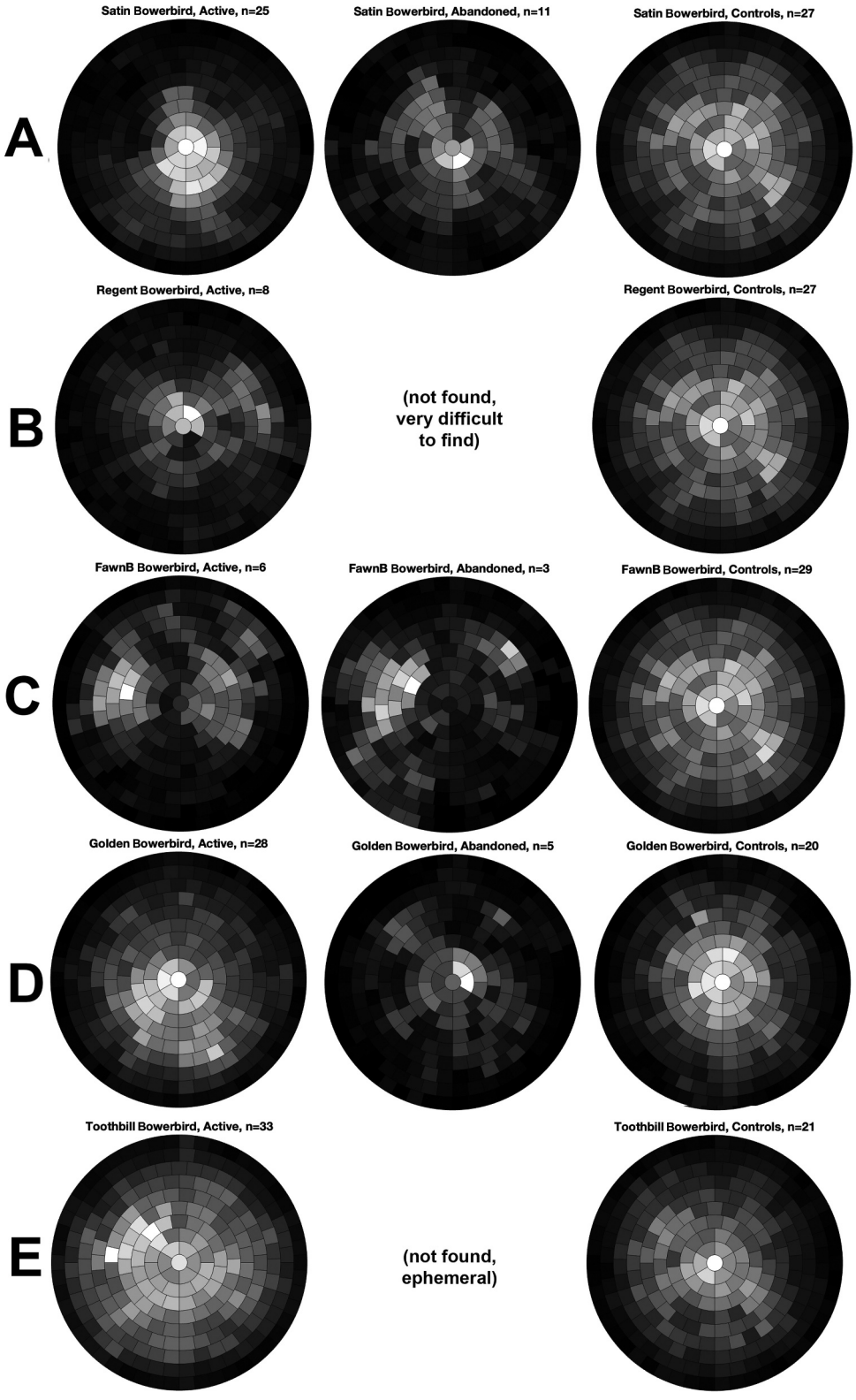

Figure 4. Relative gap fractions for rainforest Bowerbird species: (A) Satin, (B) Regent, (C) Fawn-Breasted, (D) Golden, and (E) Toothbill. The first column shows the canopy structure for active bowers, the second for abandoned bowers, and the third for control sites under the same vegetation and shrub species. Regent Bowerbird bowers are very difficult to find and are small and apparently short lived (Lenz 1999), so there are no data on abandoned bowers. Toothbill display areas consist of leaves with white undersides up, and are too ephemeral to find abandoned sites.

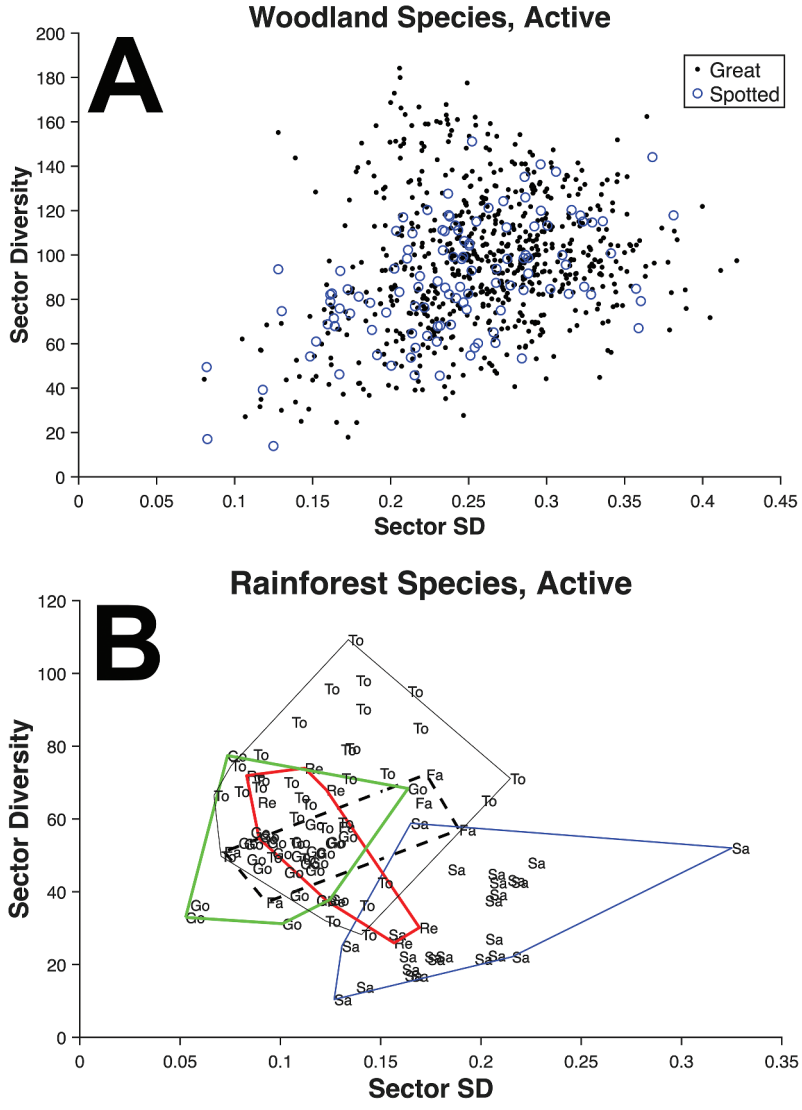

Figure 5. Sector gap fraction Hill diversity (*h*) plotted against sector gap fraction standard deviation (SD) for each species (see supplement for details on *h*). A, woodland species (Great dots, Spotted circles). B, Rainforest species (Sa Satin, to Toothbill, Fa Fawn-Breasted, Re Regent, Go Golden). Note patterns of overlap among species; woodland species overlap extensively as well as the allopatric Fawn-Breasted with other rainforest species. Sympatric species show little overlap with the Satin Bowerbird. All fraction overlaps are found in table S1 in the supplemental material.

north) overlap much less (11% South, 22% North) than the allopatric species (61% same habitat, 24% different habitats). The Fawn-breasted is found in the far north by itself and overlaps 52% in canopy pattern with rainforest allopatric species. Although the Golden Bowerbird is sympatric with the Toothbill, their bowers are very different (Frith and Frith 2004), and their canopy pattern overlaps are intermediate. The Satin Bowerbird is sympatric with the other rainforest species except for the Fawn-Breasted Bowerbird, and barely overlaps their canopy structures at all (2–16%), owing to the large canopy gap overhead.

Figure 6 shows the spatial autocorrelations among sector means for all species. There are two aspects of an autocorrelation: its plot height (correlation value *r*) and its shape. Height reflects the overall similarity among points (sectors) in the canopy, whereas shape tells us how rapidly and at what scale the canopy gap fraction changes with distance across the canopy. Steeper descent means sharper canopy gap edges, whereas slow descent means that the gaps are less distinct and have more indistinct edges (for discussion of the ambient light colour effects of gap fractions and gap boundaries, see Endler 1993). Steeper and crossing the zero line at shorter distances means smaller canopy gaps, whereas

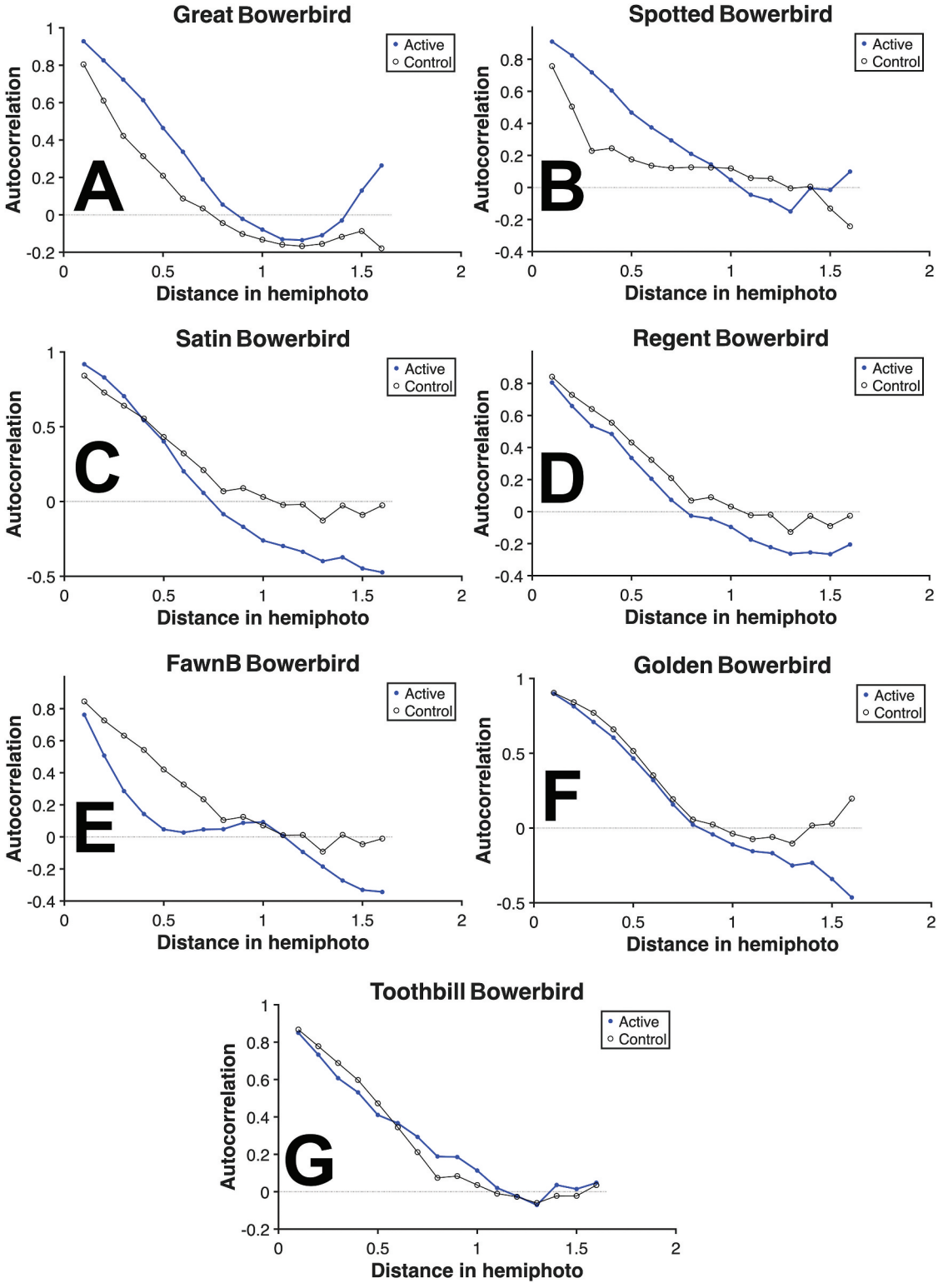

Figure 6. Spatial autocorrelations of the mean gap fractions for active Bowers (solid dots) and control sites (open circles) for each species. A Great, B Spotted, C Satin, D Regent, E Fawn-Breasted, F Golden. G Toothbill. The horizontal line is for r (correlation) = 0. Sample sizes are large so almost all the + and − r are statistically significantly different from zero. A strong positive and negative value is associated with larger differences in different parts of the canopy. See Table 1 and the supplemental material for GAMM tests for differences in autocorrelation shapes.

the same steepness further away means larger gaps. Positive followed by negative values indicate particularly strong and spatially regular gap patterns.

The differences in appearance of Great and Spotted canopies (Figure 3) are mirrored in Figure 6(A,B). The average Great Bowerbird bower canopy is more strongly defined than Spotted canopies (Figure 3(A, B), left), and this is shown by the steeper fall off and zero crossing in the Great Bowerbird autocorrelation and the gentler fall off with almost no negative values in Spotted Bowerbirds (Figure 6(A,B)). The control sites show a similar difference, but with Spotted controls, much more random. This is probably because the canopy of the shrubs over Spotted Bowerbirds, and their woodlands, is much denser than in Great Bowerbirds, at least where sampled. Similarly, for the rainforest species. Satin and Regent Bowerbirds (Figure 4(B, C); Figure 6 (C-D)) shows well-defined gaps whereas their controls (rainforest) are weaker with large scale randomness (much of r close to zero).

Fawn-breasted Bowerbirds show two gaps (Figure 4 (A)), and this is shown by their autocorrelation function with two steep components, separated by a flat component (Figure 6(E)). The Golden Bowerbird (Figures 4 (D); 6(F)) is not very different from controls except at larger distances, and the Toothbill is actually slightly more even than controls (Figures 4(E), 6(G)).

Table 2 summarises the GAMM comparisons within habitats comparing species with respect to active bowers and their control sites. The supplemental material presents the detailed results of each GAMM analysis as well as a sample R script for one analysis. A significant species factor indicates overall differences and Species-Distance interaction indicates differences in autocorrelation curve shapes. The canopy structure is significantly different among species within habitats. Interestingly the shapes of the control site autocorrelation curves are also different among species, suggesting some large-scale habitat choice within woodland or rainforest.

Microhabitat choice is suggested by comparisons between active bowers and control sites within species, as well as between active and abandoned bowers (Table 3). Autocorrelation patterns are significantly different between Active and Control sites (status) for all species except Fawn-Breasted, and between Active and Abandoned, except for Spotted, Fawn-Breasted and Regent; the latter two also have the smallest sample sizes. Significant status differences mean a more uniform gap pattern in controls. Of greater interest is significant status-distance interaction which indicates a significant difference in the shape of the decline of autocorrelation with distance, in other words, significant gap geometric pattern differences.

In summary from Table 3, Figure 6 and S2:

Great bowerbird canopies show significantly larger gaps (larger range of autocorrelation coefficients $r>0$) and more regular canopy structure than controls (drop then rise). Abandoned sites are also significantly different from active bower sites; r values declined after being abandoned (Figure S2). The large area of open canopy results in the open/cloudy light environment (whitish) in direct sunlight on the court and woodland shade (blueish) if the court is shaded (Endler 1993).

Spotted bowerbird canopies show larger and more diffuse (r goes down slowly) gaps than controls, as shown by significant differences with status and shape. Oddly, there was no difference between active and abandoned sites, but control canopies were very random. Perhaps shrub regrowth is slower in this area. The light environments on Spotted and Great Bowerbird bowers are similar, but Spotted bowers may be slightly darker and more sensitive to passing clouds (woodland shade to open/cloudy), given the slightly more diffuse gap edges (Endler 1993).

Table 2. Autocorrelation GAMM results: comparisons among species within habitats (active or controls). Full statistical test details are in the supplemental material.

	Active Bowers				Controls			
	Woodland Species: R2(adj) = 0.718, Deviance expl = 71.8%, n = 14086				Woodland Controls: R2(adj) = 0.725, Deviance expl = 72.6%, n = 2991			
Factor	edf	Ref.df	F	P-value	edf	Ref.df	F	P-value
s(Distance)	8.6731	8.9	490.27	<2e-16***	7.5786	8.044	32.276	<2e-16***
s(Species)	0.4433	1	0.796	0.00298**	0.2285	1	0.295	0.176
s(Species,Distance)	3.2860	17	1.266	0.02727*	7.1962	17	12.418	<2e-16***
	Rainforest Species: R2(adj) = 0.769, Deviance expl = 77.3%, n = 1698				Rainforest Controls: R2(adj) = 0.695, Deviance expl = 69.8%, n = 2104			
Factor	edf	Ref.df	F	P-value	edf	Ref.df	F	P-value
s(Distance)	7.547	8.164	45.542	<2e-16***	8.3903	8.848	122.252	<2e-16***
s(Species)	1.368	4	0.567	0.00476**	0.00395	4	0.001	0.484
s(Species,Distance)	21.355	44	8.124	<2e-16***	11.6956	44	1.567	<2e-16***

*$p > 0.0$; **$p < 0.01$; ***$p < 0.001$.

Table 3. Autocorrelation GAMM results: comparisons of bower condition within species. Full statistical test details are in the supplemental material.

	ACTIVE BOWERS VS CONTROLS				ACTIVE BOWERS Vs. ABANDONED BOWERS			
Effect	edf	Ref.df	F	p-value	edf	Ref.df	F	p-value
GREAT BOWERBIRD SPOTTED BOWERBIRD								
s(Distance)	8.7519	8.982	3971.42	<2e-16***	8.7319	8.979	3860.81	<2e-16***
s(Status)	0.4542	1	0.832	0.000949***	0.4712	1	0.891	3.13e-05***
s(Status,Distance)	0.4679	17	0.621	0.175991	0.4754	17	1.455	0.169
stats	R^2(ad) = 0.717. Deviance = 71.7%. N = 14378.				R^2(ad) = 0.717. Deviance = 71.7%. N = 13784			
SPOTTED BOWERBIRD								
s(Distance)	7.4235	7.917	33.278	<2e-16***	7.9387	8.701	779.971	<2e-16***
s(Status)	0.4282	1	0.749	0.00839**	0.2653	1	0.361	0.144
s(Status,Distance)	7.5424	17	11.054	<2e-16***	0.4949	17	0.044	0.264
stats	R^2(ad) = 0.736, Deviance = 73.8%. n = 2699				R^2(ad) = 0.738. Deviance = 73.9%. n = 2800.			
FAWN-BREASTED BOWERBIRD								
s(Distance)	7.4175	8.385	135.982	<2e-16***	5.00E + 00	6.678	38.57	<2e-16***
s(Status)	0.062	1	0.064	0.287	6.00E–06	1	0	0.893
s(Status,Distance)	0.0619	17	0.004	0.304	2.00E–04	17	0	0.477
stats	R^2(ad) = 0.658. Deviance = 66.2%. N = 594				R^2(ad) = 0.628. Deviance = 64.2%. N = 153			
s(Distance)	6.4572	7.062	17.191	<2e-16***	6.9471	7.899	73.081	<2e-16***
s(Status)	0.4448	1	0.801	0.0027**	0.00022	1	0	0.55
s(Status,Distance)	8.0466	17	8.779	4.03e-07***	3.0083	17	1.077	2.6e-05***
stats	R^2(ad) = 0.753. Deviance = 75.7%. n = 881				R^2(ad) = 0.798. Deviance = 80.1%. N = 607			
REGENT BOWERBIRD								
s(Distance)	6.937	7.786	26.983	<2e-16***	5.448	6.517	44.869	<2e-16***
s(Status)	0.00015	1	0	0.738	0.0644	1	0.069	0.286
s(Status,Distance)	4.0646	17	1.573	1.24e-06***	0.9744	17	0.078	0.171
stats	R^2(ad) = 0.713. Deviance = 71.9%. n = 594				R^2(ad) = 0.828. Deviance = 83.5%. N = 153			
GOLDEN BOWERBIRD								
s(Distance)	6.2355	7.227	62.827	<2e-16***	4.7099	5.319	14.552	<2e-16***
s(Status)	0.3873	1	0.632	0.0355*	0.4618	1	0.858 0	.000327***
s(Status,Distance)	3.9307	17	1.581	4.87e-05***	6.7684	17	5.655 0	.000819***
stats	R^2(ad) = 0.793. Deviance = 79.6%. N = 815				R^2(ad) = 0.802. Deviance = 80.6%. N = 561			
TOOTHBILLED BOWERBIRD								
s(Distance)	7.6407	8.406	43.378	<2e-16***	(no abandoned data)			
s(Status)	0.0003	1	0	0.692				
s(Status,Distance)	3.6516	17	2.006	<2e-16***				
stat	R^2(ad) = 0.678. Deviance = 68.2%. N = 918							

*p > 0.05; **p < 0.01; ***p < 0.001.

Satin bowerbird canopies show a large canopy gap, very different from the rest of the canopy, and a rapid drop off to negative r; there are significant differences in shape and status. Shape was significantly different between Active and abandoned; abandoned have larger holes and are more diffuse (more random). The holes mean that there will be strong light if the sun patch from the gap reaches the court, (open/cloud) and a contrast with greenish forest shade if the canopy, or part of the canopy is in shade (Endler 1993). Bowerbird males could take advantage of this contrast during displays.

Regent bowerbird canopy autocorrelation r drops faster than controls (significant distance-status interaction) and has smaller more distinct gaps than controls. Abandoned bowers were not different from controls but there was a very small sample size. It appears that abandoned have much smaller holes (Figures 4(B), 6(D)), probably caused by the vines growing over the bower after abandonment (Lenz 1999). This suggests the presence of greenish forest shade possibly interspersed with yellowish small gaps, depending upon sun angle (Endler 1993).

Fawn-Breasted bowerbird canopies show no significant differences among active, abandoned and controls, but the autocorrelation diagram (Figure 6(E)) suggests some small patches (as in Figure 4(C)) and longer distances are more random, but the small sample size makes this uncertain. The light pattern might be similar to the allopatric Regent Bowerbird.

Golden bowerbird canopies are significantly different between active, abandoned and controls in both shape and status, but this is mostly due to differences at larger distances (larger spatial scale); controls are random at larger distances, but active bowers show a decline in r over all distances. Abandoned sites are more random with smaller gaps, presumably due to canopy growth; Golden Bowerbird bowers can last for many years whereas, the other species' bowers last at most one year and their sites moved between years. The Golden Bowerbird light pattern can vary with time among forest shade, small gaps and large gaps, and

I have frequently seen this species display in sun patches from gaps. Small gaps (Endler 1993) would particularly enhance the golden colour of Golden Bowerbirds.

Toothbill bowerbird active canopies have slightly larger patches with more indistinct patch boundaries (slower decline Figure 6G) than controls. There are significant differences between active and controls in shape, slightly more uniform than controls. No data on abandoned bowers because leaves are ephemeral. Most of the light would be forest shade because the canopy is fairly continuous and apparently more regular where its structures are found.

For all species, abandoned bower canopies (Figures 3,4, S2) are mostly different from active bower canopies, possibly due to canopy regrowth, treefalls or other damage to the vegetation over the bowers between breeding seasons.

Discussion

Seven Australian bowerbirds show significant differences in the geometrical patterns of gaps in the vegetation canopy over their bowers and are significantly different from their matching control (no-bower) sites (Tables 1,2). There are also significant differences among species in general habitat, even within woodland and rainforest (Table 1). This is not surprising because canopy structure is never exactly spatially uniform within habitats. Canopy structure also changes after a bower is abandoned (Table 2, Figure S2). This is simply because vegetation is never static and constantly changes at various rates. Some changes are due to vegetation growth, resulting in a reduction of canopy gap sizes and distributions, but tree and branch falls, disease and herbivore damage can also alter the canopy gap distribution. In addition, bowers can be abandoned for two reasons: damage to the canopy by a tree fall or trampling by a cow or emu, but also because the female visitation and mating success is very low. In both cases, the wet season starts after the breeding season, and the vegetation grows actively in the wet season and affects the canopy structure. Sampled abandoned bowers are one or more years old, so it is not possible to tell the reason for abandonment unless there is a tree across the previous bower. Over the years I observed tree and branch falls over Great Bowerbird bowers followed by moving their bowers to a new site over a few days after the disturbance, but reasons for the regular movements between years are difficult to detect. However, the fact that there are significant differences between bower canopies and control (no-bower) sites under the same vegetation, and between active bower and abandoned bowers, suggests that bowerbirds are choosing bower sites using some aspects of canopy gap structure and abandoning them when the canopy becomes unsatisfactory.

Figure 5 and Table S1 suggest the possibility of a pattern of character displacement in the rainforest species because sympatric species are more different in canopy structure than allopatric species. The two woodland species are allopatric, although they form a narrow hybrid zone in the east (Frith *et al.* 1995). Except for the Fawn-Breasted Bowerbird, the rainforest species are sympatric, although there are different sympatric combinations in the north and south: Satin and Regent in the south, Satin, Golden and Toothbill in the north. Sympatric species hardly overlap in canopy structure or do not overlap even though their bowers are found within tens of metres of each other in the rainforest. Note here that I am talking about pattern, not process; conflating the two can lead to multiple problems as well as needless controversy (Stuart *et al.* 2017).

Even the existence of a character displacement pattern is weak. The number of locations for each species is too small. For a proper demonstration of the pattern, we need multiple samples within species which include both sympatric and allopatric species. Here, these data are not available and may never be because the geographic ranges of the species are too small. The pattern is just suggestive.

There is also a problem identifying the processes that may have led to the pattern. There is not enough evidence to conclusively demonstrate character displacement of bower canopy structure because there are five possible explanations for the pattern (Schluter 2000; Anderson and Weir 2021): divergence due to differences in sensory ecology, due to resource competition (character displacement proper), due to divergence in sexual selection, community assembly in which more divergent species are more likely to establish sympatry (species sorting), and random assembly. Of course, existing patterns could be due to all or some of these possible causes.

Given different possible processes, it is difficult to identify the selective mechanism for character displacement. It could be due to different sensory ecology, or differences in the sensory properties of each habitat and sensory systems of each species. The evolution of sensory systems could reflect thousands of generations of selection for (say) different visual properties which arise from local differences in food availability, food finding, predator avoidance, and mate visibility. These could

drive divergences in the Fisher sexual selection process. It could be due to resource competition where different species diverge to minimise interference for resources, including bower sites as well as food. Divergence could be due to sexual selection either for reduction of hybridisation or getting the best mate in different locations, also affecting the Fisher process. Divergence could be a simple result of community assembly where the species are already somewhat different and species that are initially more different are more likely to become partially or wholly sympatric. Finally, it could be purely random. There is simply not enough geographic variation to distinguish all of these, all that we can say here is that the pattern is weakly suggestive of some form of character displacement, for whatever cause. Any and any combination of these possible processes can produce the observed pattern. This is why it is important not to conflate pattern and process (Stuart *et al.* 2017).

There are a diversity of processes that can effect the bower location. As mentioned earlier, there are multiple selective factors for microhabitat choice, for example, what makes it easier for females to find the bower, but also what microhabitats are best for finding food or spotting approaching predators. Once the bower location is optimised then the bower structure needs to be optimised to be recognised as the correct species (if sympatric) and provide the greatest mate stimulation (as in Endler *et al.* 2014). After that, the female still has to choose. For a detailed discussion of the sequences leading up to mating, see figure 2 and accompanying discussion in Endler (2025). Any one of the links in that network of processes could lead to character displacement.

García-Navas *et al.* (2025) did a thorough phylogenetically corrected analysis of South American montane birds and found significant divergence in sympatry compared to allopatry. Their results were with respect to song, which is used in species recognition and the divergence reduces the chances of hybridisation (reproductive character displacement). Bower properties affect sound used in Great Bowerbird displays (Endler *et al.* 2024), and the vegetation canopy also affects sounds by reflecting and/or absorbing the male's sounds but also background noise (Dusenbery 1992). It would be interesting to know if there was also character divergence in bower song among the species correlated with canopy structure, although the pattern criteria are unlikely to be met.

Other studies have also had some problems identifying the cause or strongly demonstrating character displacement. Published assessments of other assemblages show that all but one of the criteria for competitive character displacement were met in more than half the cases although the interaction might not be resource based (Schluter 2000). Most cases are due to some kind of interactions among sympatric species (Anderson and Weir 2021). Martin (1998) found a significant difference between active and non-used nesting sites in birds in the southwestern USA. He found microhabitat differences in both vegetation and microclimate and nesting success was higher in preferred compared to non-preferred sites. He also found members of the same guilds were more different in microhabitat usage than species in different guilds (Martin 1998). Interestingly, character displacement is more common in the tropics, where bowerbirds are found. In any case, this is the first case of divergence of light microenvironments among sympatric species and no divergence among allopatric species living in the same habitats.

These results show the value of considering the vegetation canopy structure and the light environment as significant parts of a species' microhabitat requirements and suggest that we should do a lot more research on microhabitat properties and what cues they provide for microhabitat choice. Such information would be valuable in conservation when species use specific cues to microhabitat location. This is relatively easy in bowerbirds because they have fixed and easily accessible display sites. Other species may have ephemeral sites, or sites that are harder to find and define. Mizsei *et al.* (2024) used image analysis of places where various species of vipers were found to define habitats, and this and other image analyses techniques have promise for objective quantification of microhabitats especially if done for sympatric species. A study of microhabitat usage and consequences can result in broad conclusions of interest to general ecology and conservation. For example, Li *et al.* (2020) found that specific microhabitat usage by foraging Black Bulbuls significantly increased germination success of Chinese Yew. They found that seedling emergence increased with leaf litter cover and distance from fallen trees, and decreased with herb cover, slope and elevation. This suggests that light availability and perhaps heat from direct sunlight is most beneficial to yew seedings, as it is for other plants. Endler and Théry (1996) found that lekking cock-of-the rock chose forests with species with thin green leaves and very pale bark, and these are accompanied by saturated green light, which enhances their colour contrast. These birds defaecate on the lek sites, which tend to homogenise the species composition of those forests, reinforcing the visual effects. All these results strongly suggest that a lot more effort needs to be spent in careful observation of how species choose microhabitats during various parts of their life cycles.

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