Remotely Sensed Indicators of Habitat Heterogeneity: Use of Synthetic Aperture Radar in Mapping Vegetation Structure and Bird Habitat

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An integrated remote sensing/field ecology project linked the use of synthetic aperture radar (SAR) and aerial photography to studies of landscape spatial heterogeneity and bird community ecology. P-, L-, and C-band SAR data, collected over a section of Kakadu National Park in Australia's Northern Territory during the Joint NASA/Australia DC-8 data acquisition campaign, were analyzed in light of field data integrating vegetation structure and floristics with bird abundances across a heterogeneous study site. Results indicate that SAR data are able to discern structural differences relevant to bird habitat quality within floristically homogeneous stands, while multispectral sensors successfully identified floristic differences among habitat types. Simplifying indices of bird diversity showed ambiguous changes across the site; however, the abundances of individual species were observed to change significantly across both floristic and structural gradients. These results suggest that efforts to map bird diversity should focus on species-specific habitat relationships and that some measure of vegetation structure is needed to understand bird habitat. The approach employed here advances the use of SAR data in the three-dimensional mapping of animal habitats from remotely sensed data, and extends current capabilities for mapping and modeling large-scale patterns in the distribution of biological diversity. ©*Elsevier Science Inc., 1997*

INTRODUCTION

Plant species composition and vegetation structure are important determinants of habitat quality (Wiens, 1989). Furthermore, the spatial arrangement of different habitat types within heterogeneous landscapes has been shown to exert strong influence on the size and persistence of animal populations (Wilcove et al., 1986). Natural landscape heterogeneity, compounded by increasing rates of habitat loss and fragmentation, exerts a profound influence over the distribution of many species in heterogeneous landscapes (Wilcove et al., 1986; Wionarski et al.,1992). Fragmentation leads to a loss of habitat area and an increase of edge habitat, defined here as areas of abrupt change in vegetation cover at a scale that is relevant to the study species (Sisk and Margules, 1993). Current research suggests that, up to some minimum threshold, many species have relatively predictable responses to a loss of habitat area, while their responses to increases in edge habitat are individualistic, site-specific, and less predictable (Sisk, 1992).

Efforts to understand the effects of landscape heterogeneity and dynamic processes, such as habitat fragmentation and restoration, on animal populations are constrained by difficulties in mapping habitats at a meaningful resolution, over large areas. In particular, the characterization of vegetation structure is laborious, time consuming and expensive. Remote sensors, such as Landsat

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Thematic Mapper (TM), are being used with increasing success to classify vegetation type by floristics, but discrimination among structural types is usually not possible.

In this article, we explore the use of remote sensing technology to further our understanding of how species diversity and population density are affected by edge effects, habitat heterogeneity, and landscape composition. The primary focus of this study is an investigation of the ability of Synthetic Aperture Radar (SAR) to provide useful information on vegetation structure for the purpose of mapping bird habitats. The approach exploits the apparent ability of SAR sensors to respond to vegetation structure. In boreal and coniferous temperate forests, tree stand parameters such as height, stocking density, and sometimes leaf area can be inferred using polarimetric radar and classification algorithms employed to map stands (Dobson et al., 1993, 1995; Ranson and Sun, 1994; Ranson et al., 1995). Biomass mapping using SAR has also met with some success, although the application and saturation level varies, depending upon the forest type. See Dobson et al. (1992, 1995), Kasischke (1992), LeToan et al. (1992), and Israelsson et al. (1994) for temperate forests and Hoekman et al. (1995), Pope et al. (1994) and Imhoff (1995a) for tropical forests and comparisons to temperate coniferous stands. SAR sensor data has also been used to monitor gross vegetation habitat parameters for conservation purposes (Lawrence et al., 1995). Using SAR data, it may be possible to distinguish among several different vegetation structural archetypes that often have pronounced effects on bird distribution and abundance. We examined the working hypothesis that SAR responds to vegetation structure in predictable ways, based on wavelength and the degree of consolidation of living plant tissue. Past research has shown that SAR backscatter is linked to vegetation structure, and that the ratio of vegetation surface area to volume may be a useful measure of structural consolidation (Imhoff, 1995b). If SAR can discriminate among vegetation structural types, and this information is layered onto floristic data acquired from aerial photography, Landsat TM, and other sensors, the potential for high resolution mapping of animal habitats, over large areas, is immense.

SITE DESCRIPTION AND REMOTELY SENSED DATA

To test the hypothesis that SAR could add meaningful structural information to habitat characterization efforts, we sought a study site that met the following criteria: 1) a mix of different habitats abutting at distinct edges, 2) edges that show substantial vegetation structural changes in the absence of major floristic differences, and 3) other edges that show distinct floristic changes in the absence of major structural differences. By isolating floristic and structural changes, we could evaluate the ability of the SAR to discern these different habitat attributes.

A study area was identified in the Northern Territory of Australia, where abrupt structural and floristic edges are sustained by edaphic conditions near the South Alligator River in Kakadu National Park (12.5°S Lat./132.5°E Long.) (Fig. 1). The area has a tropical hot-wet/hot-dry climate with 85–95% of its 1400 mm of precipitation occurring between December and March. Maximum daily temperatures are +30°C all year. It is characterized by a flat estuarine flood plain leading to the Arafura Sea, with freshwater billabongs, paleosol (laterite) uplands and sandstone ridges and outcrops scattered throughout. Although there currently is relatively little human activity in the area, impacts from prior human habitation are evident in the form of sizable populations of feral animals and some exotic flora. Fire of natural and anthropogenic origin is a major part of the ecosystem dynamics throughout the region.

The study area is characterized by two primary floristic types; a paperbark (*Melaleuca* spp.) stand located on the wet lowland soils, which diminishes in stature as it approaches the upland, and a mixed woodland composed of *Eucalypts* and other broadleaf species. There are two structural edges in the *Melaleuca* forest. One distinct change occurs where the perennially flooded soil line is located and another midway toward the uplands. The edge located at the perennially flooded soil boundary is identified as Edge A and is primarily a structural edge, meaning that species composition is similar on both sides, but the size and architecture of the stand changes markedly. A distinct floristic edge occurs at the upland boundary, defined by the furthest extent of flooding in the wet season. The *Melaleuca* woodland abruptly terminates at this point and is replaced by the mixed *Eucalypt* woodland. This floristic edge is denoted as Edge B. Reference data are available on species composition and habitat functional groups for this site and the Kakadu area in general [see Taylor and Dunlop (1985) and Wilson and Bowman(1987) for vegetation and Woinarski et al. (1992), Whitehead et al. (1992), and Woinarski and Braithwaite (1993) for bird and habitat studies].

In September 1993, P-, L-, and C-band SAR data were collected over the study site as part of the Joint NASA/Australia AIRSAR Deployment. Flight line azimuth was straight north. The habitat edges run roughly east–west in orientation across a radar range of about 5° (52–57° incidence angle). The incidence angles used are not considered ideal, but the location of the final flight line relative to the best study sites precluded use of lower angles. The vegetation structural gradient changes in a north–south direction, which is the azimuth direction of the radar and therefore not subject to the large changes in incidence angle that result from range location in airborne SAR. The SAR data were supplemented by Landsat TM imagery captured 12 days earlier and a 1:25,000 scale color aerial photo taken in May 1991. The TM data were used in an image interpretative way, pri-

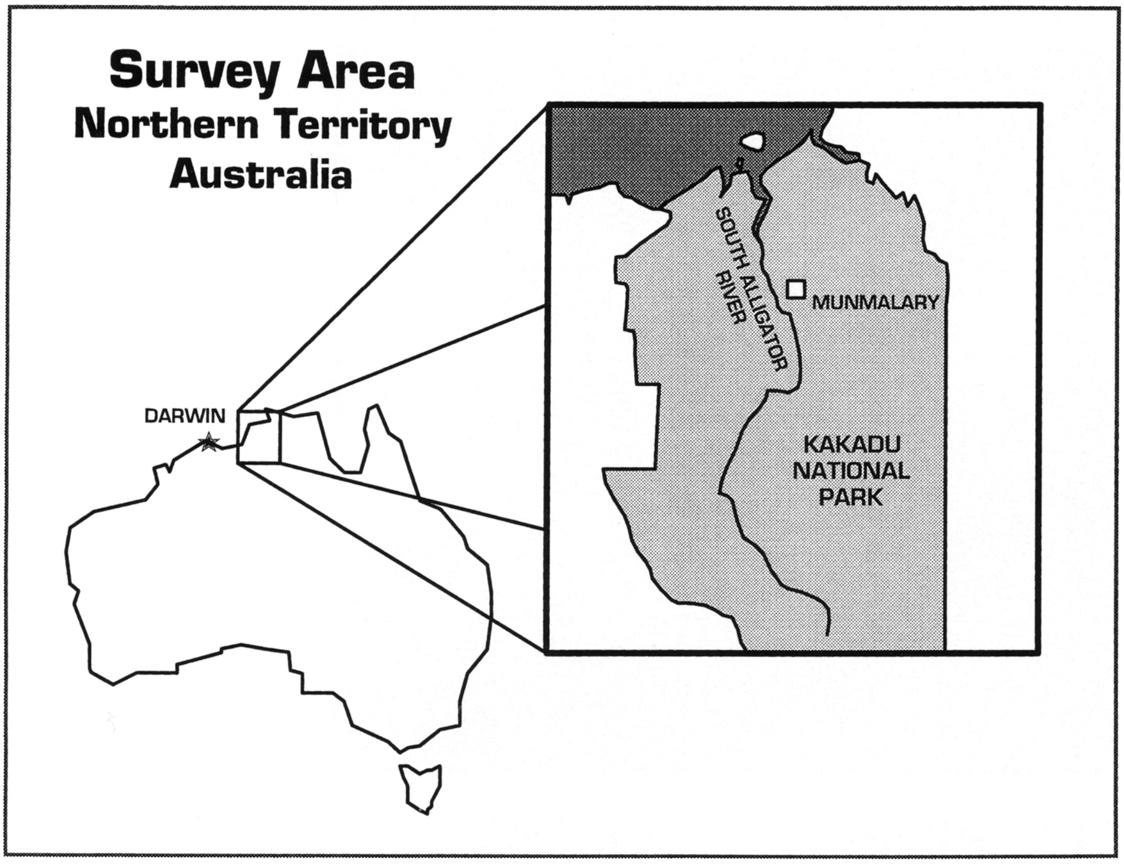

Figure 1. Location of Munmalary study area in Kakuda National Park, Northern Territory, Australia.

marily to verify the classes of vegetation at the site, and the air photo was used to lay out transects (Table 1). The SAR and TM data were collected late in the dry season, and the air photo was taken at the beginning of the dry season.

METHODS

In August–September 1994 we collected field data on vegetation structure, floristic composition, and bird abundances. The data were collected along transects running orthogonal to the habitat edges (parallel to the flight line). The study area encompassed approximately 1.5 km^2 (Fig. 2).

Table 1. Remote Sensing Data Available for the Munmalary Study Area, Kakadu National Park, Northern Territory, Australia

NASA/JPL AIRSAR	C-, L-, and P-Band Quadpol. $\theta_i = 55°$	24 September 1993
Landsat TM[a]	Path 105, Row 69	12 September 1993
Color air photo	1:25,000 scale	May 1991

[a] Landsat TM was used primarily in a photo interpretative way for this study.

Bird Survey

Ten north–south trending transects were established at random locations with a minimum separation of 100 m and a maximum separation of 300 m. Along each transect, survey points were placed systematically at intervals of 100 m. These spacings were chosen to minimize the probability of counting individual birds more than once during a survey period. The southernmost point was established 200 m south of the edge between the wet *Melaleuca* and dry *Melaleuca* woodland (Edge A) and extended 200 m north of the edge between dry *Melaleuca* and mixed *Eucalypt* woodland (Edge B). Transects varied in length from 0.5 km to 1.5 km, depending on the width of the dry *Melaleuca* woodland band (see Fig. 2). Each transect was surveyed twice (between 0.5 h before sunrise and 3 h after sunrise) over 10 consecutive days, once beginning at the northern end of the transect and once beginning at the southern end. Two transects were selected arbitrarily each morning, and specific pairings of transects were not repeated. At each point, 5-min stationary counts were conducted using established variable circular plot techniques (Reynolds et al., 1980; DeSante et al., 1981). All birds seen or heard were recorded, along with an estimate of their distance from the survey

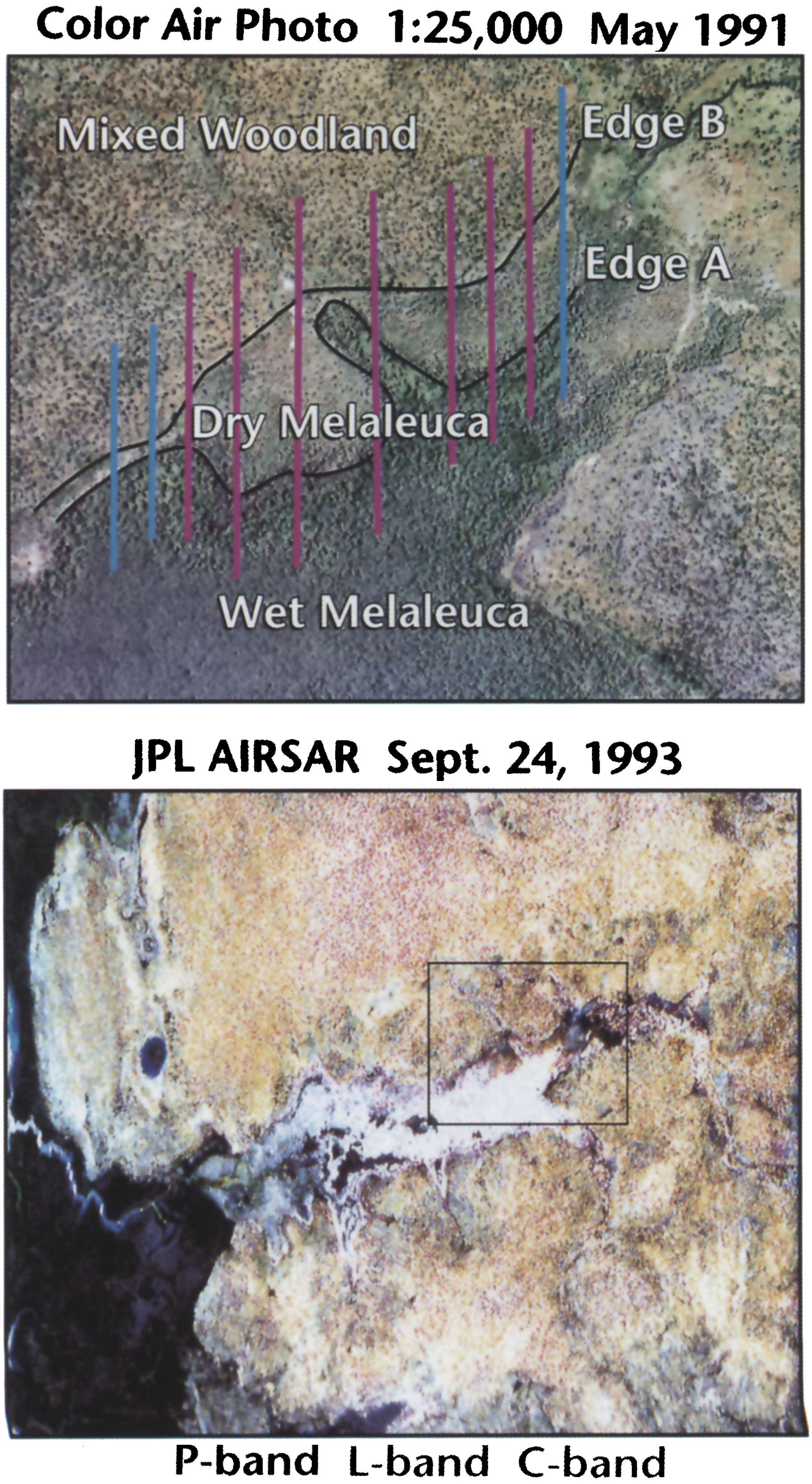

Figure 2. Study site and sampling design for the survey area. Aerial photography was used to verify the vegetation floristic classes and their spatial relationships across the survey area. SAR imagery was used to quantify structural attributes of the vegetation, contributing to a three-dimensional view of avian habitat types.

point, up to a maximum of 50 m. Birds detected at distances greater than 50 m were not included in the analyses presented in this article.

Two community-wide indices of bird diversity were calculated. Species richness is used to measure alpha diversity at regular intervals along the habitat gradient (Pielou, 1966). The Jaccard index of similarity (C_J) is used to measure beta diversity, the degree of turnover in species composition between two adjacent points along the gradient (Ludwig and Reynolds, 1988). Additional analyses focused on abundance patterns for individual bird species. Abundance, represented by the number of detections per point count, was plotted against the position of the point along the habitat gradient. The frequency of detection within 150 m of each edge was tested against a uniform distribution (G-test) to identify significant changes in abundance. In all cases, a probability of $p<0.05$ was deemed sufficient to reject the null hypothesis that the detections were distributed randomly along the gradient (Sisk, 1992; Sisk and Margules, 1992).

Vegetation Sampling

Vegetation data were collected using the point-center-quarter (PCQ) method (Mueller-Dombois et al., 1981) along seven of the 10 bird transects. Point data were taken at 33 m intervals so that each of the bird observation points would be sampled and flanked by a vegetation PCQ point on either side. The data collected included: species, stem diameter (dbh), height, height to live crown, crown dimensions in three dimensions, and stocking density. In all, 190 PCQ samples were taken, compiling measurements for over 760 individual trees. Estimates for crown components, such as branch length, diameter, and number of branches, were made using photographic methods on selected trees. Five trees for each of the dominant species spanning the range of recorded diameter and heights were photographed with a height and diameter reference visibly marked on the tree and the diameter, height to marker, height to live crown (first branching), total height and crown dimension (as described above), measured and recorded in a log book. Branch number, dimensions, and angle (modeled as cones) were estimated by measurement from the photographs using proportions from the known quantities and then applied by allometric scaling to the rest of the trees measured, as a function of diameter and height class. This technique allowed a crude but effective way of estimating the crown component of stands, given a limited field budget and staff. Bulk densities (wood) for the various species were derived from Bootle (1983) and used to compute biomass values from bole and branch volumes.

Leaf area index (LAI) was estimated, using hemispherical canopy photography and the CANOPY software program (Rich, 1989). Hemispherical canopy photography and crown photos were taken at each PCQ point. The field data were collected at the end of the dry season, approximately one year after collection of the SAR data. Undergrowth was minimal, and many deciduous trees in the mixed woodland were without leaves.

Habitat Zones

Bird and vegetation data were grouped into nine 100-m-wide zones running parallel to Edges A and B. Zone 1 represents the interior of the perennially wet *Melaleuca* forest and Zone 9 represents the interior of the mixed *Eucalypt* woodland. Zone 3, for example, is a 100-m-wide band of wet *Melaleuca* forest with its northern boundary coincident with that of the perennially flooded soil, forming the south side of Edge A. Zone 4 includes dry *Melaleuca* woodland outside the perennially flooded boundary, and so on. Edge B, the floristic edge, is bounded by Zones 6 and 7. Each zone contains a minimum of 21 PCQ points. This equates to a minimum of 84 samples per zone (except for stocking density, where one PCQ point yields one density measure). Statistics are reported for floristic composition and vegetation structure, including mean stem density, dbh, height, biomass, and the ratio of vegetation surface area to volume (SA/V) for each of the nine zones. Structural differences between zones were determined using a mean difference unpaired *t*–test, where a value of $p<0.01$ was deemed sufficient to reject the null hypothesis that the values did not differ.

SAR Data Analysis

The SAR data were geometrically corrected using the PCI image processing software and backscatter statistics were calculated using the MacSigma0 software package (Norikane, 1993). Backscatter is reported as σ° in dB (m^2/m^2) and backscatter statistics for each SAR channel (means and standard deviations) were collected for each zone by defining their boundaries on the SAR image and computing statistics from the backscatter recorded for each pixel. Locating zone boundaries on the SAR data was simplified by the fact that the edges could be easily observed on the SAR images. There were more than 200 SAR pixels in each zone. In order to identify the SAR channels most likely to delineate needed vegetation structural parameters, a regression analysis was performed relating the SAR backscatter for each channel and the measures of vegetation structure. SAR channels showing highest correlations with structural parameters were selected. C-band was used to define canopy parameters, L-band for branch parameters, and P-band for stem parameters. The selected channels were then tested to determine whether the observed differences in backscatter between zones were statistically significant (Z–test; $a=0.01$, $N\geqslant 200$ in all cases).

Table 2. Vegetation Structural Summary by Zone[a]

	Edge A					*Edge B*			
Zone	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*
Dominant Species % of All Individuals	*Mel. caj.* 82%	*Mel. caj.* 57%	*Mel. caj.* 68%	*Mel. caj.* 82%	*Mel. viri.* 66%	*Mel. viri.* 59%	Mixed *Eucal.*	Mixed *Eucal.*	Mixed *Eucal.*
No. of trees/100 m^2	3.60	3.98	2.83	4.57	6.84	5.20	4.54	4.25	4.87
Mean dbh (cm)	32.21	34.42	34.26	**19.20**	**10.20**	11.14	14.29	12.75	12.30
Mean hgt (m)	14.25	12.77	13.15	**9.72**	**6.08**	6.67	6.43	6.59	7.27
Mean bole vol. (m^3)	0.87	0.76	0.84	**0.28**	**0.06**	0.06	**0.13**	0.09	0.08
Mean bole SA/V (m^2/m^3)	23.70	19.11	23.73	**33.19**	**53.77**	50.38	47.70	52.59	46.16
Mean total branch volume (m^3)	0.113	0.133	0.133	**0.013**	**0.007**	0.003	**0.016**	0.011	0.010
Mean branch SA/V (m^2/m^3)	22.80	20.75	20.63	**85.94**	**241.39**	254.65	**99.07**	127.81	141.26
Total dry BM (kg/m^2)	26.52	26.76	20.73	**10.04**	**3.54**	2.54	**6.79**	4.44	4.20
LAI (m^2/m^2)	1.41	1.51	1.32	**0.61**	**0.35**	0.36	0.40	0.27	0.35

[a] Zones run parallel to the habitat edges starting with Zone 1, 200 m from Edge A in the perennially wet *Melaleuca*, progressing northward to Zone 9, 200 m beyond Edge B in the Mixed *Eucalypt* stand. All zones had a minimum of 21 PCQ samples. **Bold entries** denote a significant change in the listed structural parameter from that of the previous zone. The statistical significance of differences in vegetation structure between zones was tested using a mean difference unpaired comparison *T*-test ($p < 0.01$, DF $\geq$ 84 in all cases). Dominant tree species per zone: Zones 1–4, *Melaleuca cajuputi*; Zones 5 and 6, *Melaleuca viridiflora*; Zones 7–9, mixed *Eucalypt*.

RESULTS AND DISCUSSION

Vegetation Structure of the Habitat Zones

Statistical analysis of the vegetation field data clarified the structural and floristic changes across the study site. A distinct structural edge occurred in the absence of changes in dominant tree species at Edge A (transition between Zone 3 and Zone 4), where a *Melaleuca cajuputi* woodland changed from a tall, closed canopy (Zones 1–3) to a formation of smaller individuals (Zone 4). All of the structural parameters except stem density changed significantly across Edge A (Table 2). Another statistically significant structural change occurred between Zones 4 and 5, where the *Melaleuca cajuputi* dominant stand (Zone 4) changed to an even smaller structured stand containing a mixture of *M. viridiflora* (dominant) and *M. cajuputi* (Zone 5). Almost certainly, this change is driven by edaphic factors, with *M. viridiflora* favoring drier soil.

At Edge B, the *M. cajuputi* woodland gave way abruptly to a mixed woodland of *Ecualypts* (*Eucalyptus tectifica*, *E. confertiflora*, and *E. papuana*, in order of abundance) and other broadleaf evergreen (chiefly *Terminalia* spp.) and deciduous species. While the floristic change at Edge B is very abrupt and nearly absolute, many of the primary structural parameters measured did not change significantly across this obvious edge (Table 2). Tree density, mean dbh, and height did not change. There was a marginal change in bole volume across Edge B (significant with p-value=0.005) but the Bole SA/V did not change significantly (p-value= 0.924). Crown parameters, such as mean total branch volume and branch SA/V however, did show some changes. Bole biomass also changed at Edge B, but this may be due more to the higher bulk density of *Eucalypts* (approximately 1070 kg/m^3 dry for *Eucalypts* compared to 750 kg/m^3 dry for *Melaleuca*) than to the difference in bole volume (see Table 2). Thus, the floristic Edge B (transition from Zone 6 to 7) showed relatively few structural differences, considering the complete change in species composition.

Vegetation Structure and SAR Response

All three SAR bands (C-, L-, and P-) had channels that responded predictably to changes in key vegetation structural features. C-HV was correlated to LAI (R^2=0.987, p-value < 0.0001), L-VV was correlated to branch SA/V (R^2=0.849, p-value=0.0004), and P-VV had a strong relationship with bole SA/V (R^2=0.846, p-value=0.0004) (Fig. 3). The prevalence of like-polarized VV and cross-pol channels in the correlations to vegetation structure may be due to the high incidence angles in the radar data. Crown features, such as the size and angular distribution of branches and leaves, will have a greater influence at the more oblique angles since the path length is longer through the crown than at lower incidence angles. HH backscatter for all bands had disappointingly low R^2 values for all structural measures, again probably due to a diminished contribution from the bole and bole–ground interactions at the large angles.

The mean SAR backscatter for all bands (C-HV, L-VV, and P-VV) showed statistically significant changes (Z-tests; a=0.01, see Table 3) at Edge A, the main struc-

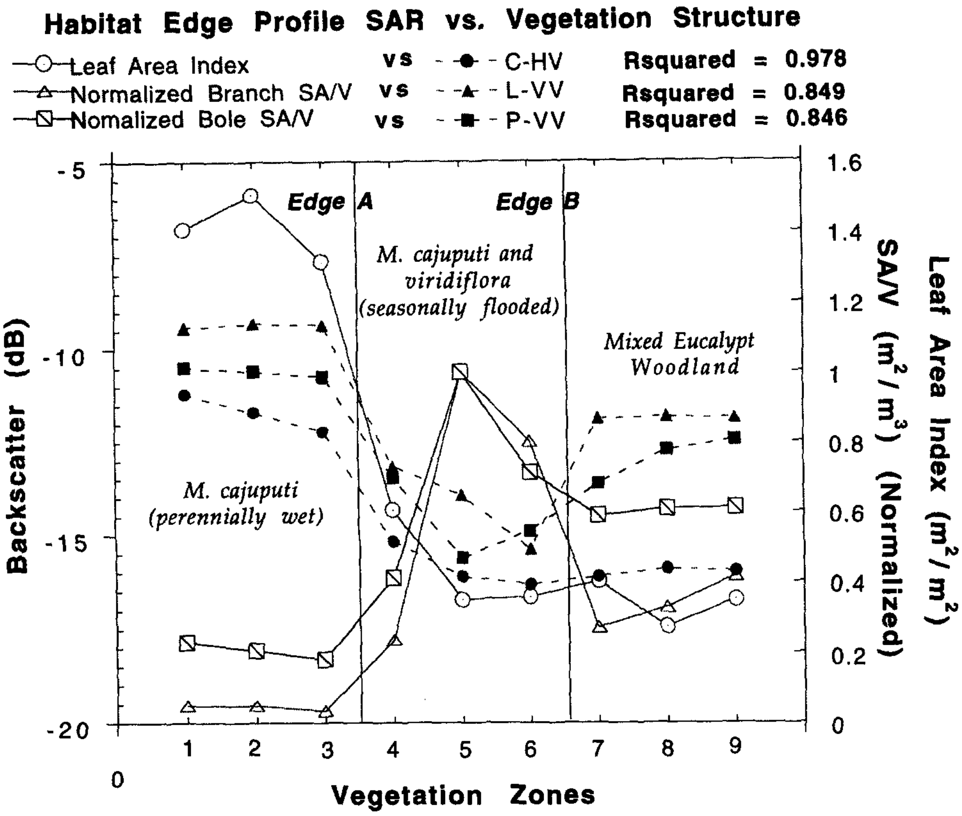

Figure 3. SAR response to vegetation structure along the habitat gradient quantified in nine zones. All changes in structural parameters except stem density were significant across Edge A and at Zone 5, despite their nearly monospecific composition ($p < 0.01$, t-test unpaired comparison). Few structural changes were statistically significant across Edge B except, notably, Branch SA/V. The SAR channels shown responded significantly (Z-test, $\alpha=0.01$) to changes in crown parameters at Edge A, Zone 5, and Edge B. (see Table 3).

tural edge, and again at Zone 5, where the other structural change occurred in the floristically similar *Melaleuca*-dominated stands in Zones 4–6. The C-HV channel responded strongly to LAI in all zones, and backscatter changed significantly at Edge A and at Zone 5, where LAI also showed statistically significant changes (Table 2). C-HV did not show a significant change in backscatter at Edge B, nor did LAI change significantly. Because these data were collected in the dry season, the leaf area present in all zones was quite low (below 1.5 m^2/m^2), reducing the likelihood of signal saturation.

At Edge B, the SAR backscatter again responded strongly to the significant crown-related structural changes occurring at Edge B (notably Branch SA/V). L-band (L-VV) responded most strongly to branch SA/V and the P-VV channel also showed a high correlation with this crown structural measure (P-VV to Branch SA/V: $R^2=0.817$, p-value$=0.0004$). The longer wavelengths responded to both crown and bole components and were most highly correlated with the SA/V measures of each. The strong relationship between L- and P-band backscatter to the crown component could be, again, due to the large incidence angles as much as the correlation among biometric measures. Analysis of additional SAR data, acquired at lower incidence angles, could help resolve this question (see Table 3 for Z-test results for the SAR channels and habitat edges).

Birds and Vegetation Structure

Over the 10-day survey period, 1449 positive identifications were made of birds representing 58 species. Of these, nine species were detected more than 40 times permitting robust analysis of abundance patterns (see Appendix). The mean number of bird species detected in the nine vegetation zones (alpha diversity) ranged from 6.0 to 8.4, with high variation within zones (Fig. 4).

Table 3. Changes in SAR Backscatter (dB) for Selected Channels across Three Habitat Edges (Z-test, $\alpha=0.01$, $N>200$ in all cases).

	Z-Values		
SAR Channel	Edge A (Zones 3–4)	Second Structural Edge (Zones 4–5)	Edge B (Zones 6–7)
C-HV	23.12*	6.96*	1.64
L-VV	30.07*	5.80*	27.18*
P-VV	23.37*	17.55*	9.57*

* $p < 0.01$.

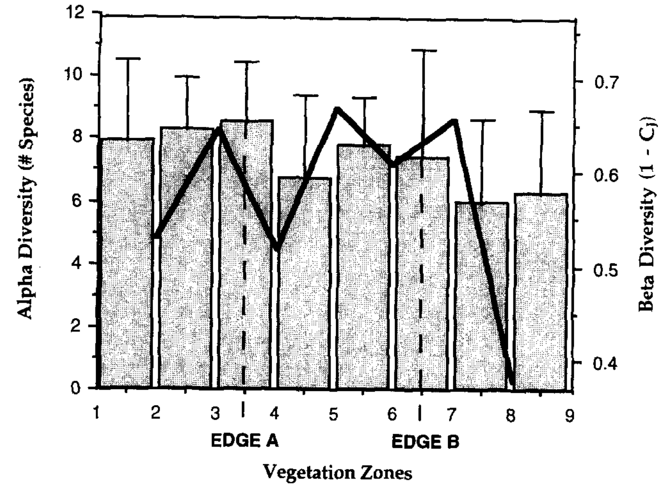

Figure 4. Patterns in alpha and beta diversity differed greatly across the habitat gradient. Alpha diversity, as measured by species richness (bars), remained relatively constant across the study site, while beta diversity, measured as the proportion of species that differed between adjacent zones ($1\text{-}C_j$, thick line), fluctuated independently of floristic and structural changes in the vegetation. Error bars are standard deviations from the mean number of species detected in each vegetation zone.

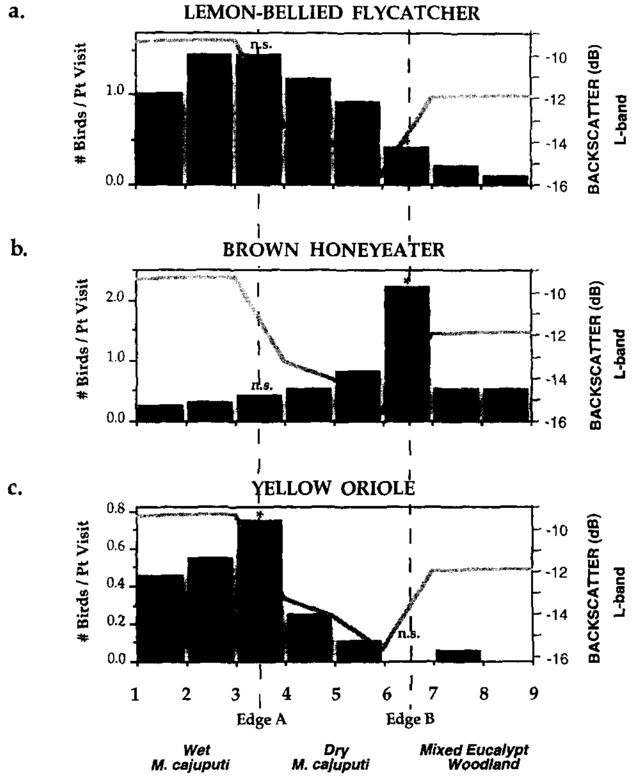

Figure 5. Changes in the abundances of three bird species across a habitat gradient ranging from wet *Melaleuca* woodland (Zones 1–3), through dry *Melaleuca* woodland (Zones 4–6), to mixed *Eucalypt* woodland (Zones 7–9.) Abrupt edges between these habitat types occurred at Edge A and Edge B. Frequencies of detection across each edge were tested against a uniform distribution ($^*p \leq 0.05$; n.s.=not significant). Dark lines illustrate the relationship between SAR L-band backscatter, bird abundances, and floristics. Within wet *Melaleuca*, L-band is relatively constant, as are bird abundances. A pronounced structural gradient within the dry *Melaleuca* is mirrored in bird abundances in panels a and c, while structure and birds are again relatively unchanging within *Eucalypt* woodland. Brown honeyeater shows little response to either floristic or structural gradients, but has a strong positive association with Edge B, which is clearly evident in SAR data. C- and P-bands capture different aspects of vegetation structure. See text.

Rates of turnover in species composition (beta diversity) also varied greatly, with no consistent trend across the study site (Fig. 4). These data suggest that commonly employed community indices convey little information about the complex changes in bird diversity observed across this highly heterogeneous study site. The key factors in this case are not how many, but which species are present in the different vegetation types. Different species showed widely varying responses to both structural and floristic changes along the habitat gradient. Of the nine species detected more than 40 times, abundances for two species differed significantly only between the structurally distinctive wet and dry *Melaleuca* zones, while abundances for three species differed between the floristically distinct dry *Melaleuca* and mixed *Eucalypt* woodland. Three other species showed significant differences among all three vegetation types, while one species was equally abundant in all three types. Of these nine species, four were significantly more abundant at one or both edges than in either of the adjoining habitat types, while five species showed no change in abundance attributable to habitat edges. What emerges from these results is a complex pattern of species-specific responses to structural and floristic characteristics of avian habitat, patterns that are not easily generalized across species. Other authors have reported similarly complex responses for birds and other mobile taxa in Australia's Northern Territory (Wionarski and Tidemann, 1991; Wionarski et al., 1992; Wionarski and Braithwaite, 1993) and elsewhere (see Wiens, 1989).

Here we present data for three species that illustrate the range of -species-specific responses observed across the habitat gradient. A more comprehensive analysis of avian community dynamics will be provided in a subsequent publication.

The lemon-bellied flycatcher (*Microeca flavigaster*) responded primarily to floristics (Fig. 5a). It was associated with habitats dominated by both *Melaleuca* species, and its abundance did not change significantly at the structural edge (Edge A) between the wet and dry *Melaleuca* woodland. At Edge B, where vegetation structure did not change markedly but where the *Melaleuca*-dominated woodland was replaced by the mixed woodland dominated by ***Eucalypts***, the species declined significantly ($p<0.05$, G-test). The brown honeyeater (*Lichmera indistincta*) occurred abundantly throughout the study site (Fig. 5b). Its density did not differ markedly among vegetation types; however, its significant increase at Edge B ($p<0.05$) suggests that floristic aspects of its habitat may be important. The yellow oriole (*Oriolus flavocinctus*) appears to be strongly associated with wet *Melaleuca* forests (Fig. 5c). Within this habitat it occurred with greater frequency at the edge. This species appears to be responding strongly to both floristic and structural elements, generating a more complex edge-associated response.

At this site, and in many heterogeneous landscapes, the within-habitat variation in species diversity is high, making it difficult to extract a simple message that is relevant to conservation planning (Sisk and Margules, 1993). Bird species display varied and individualistic responses to habitat heterogeneity and management decisions must take into account these characteristic responses. Some species, illustrated here by the lemon-bellied flycatcher, respond strongly to floristics. Such responses may be driven by food availability, cover, perching or nesting sites, and other factors related to the species composition of the plant community. Other species, such as the brown honeyeater, appear to key on edges and other structural and / or spatial aspects of the habitat. Many species show detectable responses to both floristics and structure and, like the yellow oriole, show more complex patterns of abundance associated with multiple factors. Of course, most species respond to a combination of factors, and it is likely that few are insensitive to radical changes in either floristics or vegetation structure.

The overlaying of SAR data with floristic information illustrates the degree to which structural data may help explain changes in bird abundances across the study site. Lemon-bellied flycatcher (Fig. 5a) and yellow oriole (Fig. 5c), both canopy species, decline in abundance as L-band backscatter, indicative of canopy and branch architecture, decreases in the dry *Melaleuca* woodland. Both species are rare in the floristically distinct mixed *Eucalypt* woodland, despite intermediate SAR signatures and canopy architecture in Zones 7–9. Abundance of brown honeyeater (Fig. 5b), a generalist found in all vegetation layers, does not track L-band or any SAR channel but is positively associated with floristic edges. This study demonstrates that the relative importance of vegetation structure and species composition differs among species, suggesting that knowledge of both factors is essential for understanding avian habitats.

Maps of vegetative communities, commonly produced from Landsat and similar spectral imagery, do not in themselves constitute habitat maps. Structural data are also needed. Currently, these data are available only through the laborious and expensive collection of extensive field measurements. SAR technology offers the possibility of acquiring a structural layer from remotely sensed data (Kasischke and Christensen, 1990; Paris, 1986).

CONCLUSION

Our results confirm that SAR data is capable of discerning vegetation structural changes that can be significant contributors to avian habitat quality. The high incidence angles used in this study resulted in an enhanced sensitivity to crown components, which changed significantly at the habitat edges. The use of smaller incidence angles might have resulted in L- and P-band backscatter that was less sensitive to the crown and more responsive to larger branches and bole size and spacing. Combining incidence angles in this case could provide a complete picture of the stand structure where P- and L-band backscatter (at the smaller incidence angles), might not have changed across Edge B, where much of the branch and bole geometry remained constant across the floristic boundary. Ideally, the use of multiple angles could allow the separation of these responses and clarify the influence of structural features.

Results from this study also indicate that bird species are individualistic in their responses to habitat heterogeneity and that edges are potentially powerful factors in determining the distribution and abundance of bird species in heterogeneous landscapes. Through the integration of SAR, multispectral, and field data, we were able to isolate trends in floristic and structural components of bird habitats. We found that bird species responded individualistically to structural features, and that SAR data are capable of identifying these features. The combination of SAR and multispectral data may provide the foundation for a new generation of remote sensing tools for mapping wildlife habitats. Ultimately, these maps, when combined with species-level ecological data, should permit better predictions of the distribution and abundance of birds and other species of conservation interest in heterogeneous landscapes.

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APPENDIX

Bird species detected at the Munmalary study site and the number of observations for each. Kakadu National Park, Northern Territory, Australia.

Little egret	*Egretta garzetta*	1
Intermediate egret	*Egretta intermedia*	2
Jabiru	*Xenorhynchus asiaticus*	1
Sacred ibis	*Threskiornis aethiopica*	22
Straw-necked ibis	*Threskiornis spinicollis*	1
Magpie goose	*Anseranas semipalmata*	16
Grey goshawk	*Accipiter novaehollandiae*	1
Peaceful dove	*Geopelia placida*	150
Bar-shoulder dove	*Geopelia humeralis*	117
Sulfur-crested cockatoo	*Cacatua galerita*	4
Red-collared lorikeet	*Trichoglossus rubitorquis*	151
Varied lorikeet	*Psitteuteles versicolor*	13
Red-winged parrot	*Aprosmictus erythropterus*	4
Brush cuckoo	*Cuculus variolosus*	6
Tawny frogmouth	*Podargus strigoides*	5
Blue-winged kookaburra	*Dacelo leachii*	31
Forest kingfisher	*Halcyon macleayii*	17
Sacred kingfisher	*Halcyon sancta*	1
Rainbow bee-eater	*Merops ornatus*	26
Black-faced cuckoo-shrike	*Coracina novaehollandiae*	3
White-bellied cuckoo-shrike	*Coracina papuensis*	26
White-winged triller	*Lalage sueurii*	26
Varied triller	*Lalage leucomela*	5
Lemon-bellied flycatcher	*Microeca flavigaster*	148
Rufous whistler	*Pachycephala rufiventris*	73
Little shrike-thrush	*Colluricincla megarhyncha*	1
Broad-billed flycatcher	*Myiagra ruficollis*	9
Leaden flycatcher	*Myiagra rubecula*	3
Shining flycatcher	*Myiagra alecto*	9
Paperbark flycatcher	*Myiagra inquieta*	15
Rufous fantail	*Rhipidura rufifrons*	8
Northern fantail	*Rhipidura rufiventris*	9
Willie wagtail	*Rhipidura leucophrys*	12
Weebill	*Smicorornis brevirostris*	11
Black-tailed treecreeper	*Climacteris melanura*	1
Silver-crowned friarbird	*Philemon argenticeps*	15
Little friarbird	*Philemon citreogularis*	8
Blue-faced honeyeater	*Entomyzon cyanotis*	4
White-gaped honeyeater	*Lichenostomus unicolor*	19
White-throated honeyeater	*Melithreptus albogularis*	70
Brown honeyeater	*Lichmera indistincta*	108
Bar-breasted honeyeater	*Ramsayornis fasciatus*	5
Rufous-banded honeyeater	*Conopophila albogularis*	76
Rufous-throated honeyeater	*Conopophila rufogularis*	10
Dusky honeyeater	*Myzomela obscura*	28
Mistletoebird	*Dicaeum hirundinaceum*	20
Striated pardalote	*Pardalotus striatus*	3
Long-tailed finch	*Poephila acuticauda*	13
Yellow oriole	*Oriolus flavocinctus*	49
Olive-backed oriole	*Oriolus sagittatus*	10
Australian magpie-lark	*Grallina cyanoleuca*	11
Grey butcherbird	*Cracticus torquatus*	3
Torresian crow	*Corvus orru*	21

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