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Scale relationships and linkages between woody vegetation communities along a large tropical floodplain river, north Australia

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Abstract: Riparian vegetation varies according to hydrogeomorphic processes operating across different scales over two didmensions: transversely (across-stream) and longitudinally (parallel to stream). We tested the hypothesis that vegetation patterns reveal the scale and direction of underlying processes. We correlated patterns of dominant woody vegetation with environmental variables at 28 sites located within four geomorphologically distinct regions along the length of the South Alligator River catchment of Kakadu National Park, northern Australia. Across the catchment there existed a strong transverse boundary between upland savanna vegetation and two zones of riparian vegetation: *Melaleuca*-spp.-dominated closed-forest vegetation along stream channels and mixed open-woodland vegetation adjacent to closed forest. We surmise that there is hierarchic constraint on smaller-scale catchment processes due to fire incursion into the riparian zone and access to water during the dry season. Within the closed-forest zone, vegetation did not vary transversely, but did longitudinally. Riparian woodlands also varied longitudinally, but in the upper reaches varied independently of stream variables. By contrast, in the lower reaches woodland was strongly correlated with stream variables. The observed pattern of weak transverse linkages in headwaters but strong linkages in lower reaches is analogous to models developed for in-stream patterns and processes, particularly the river continuum and flood-pulse concepts.

Key Words: Flood-pulse concept, hierarchical processes, Kakadu National Park, landscape pattern, *Melaleuca*, riparian fire regimes, river continuum concept, tropical savanna, vegetation distribution, wet–dry tropics

INTRODUCTION

The relationship between hydrology, geomorphology and riparian vegetation has long been of interest to ecologists. It is well known that riparian plant community composition varies as species respond to longitudinal changes in geomorphological processes, channel constraint and fluvial regimes. The topographical variation of transverse stream profiles determines water table access during low flows and the period and depth of inundation during high flows (Hupp & Osterkamp 1996), and influences disturbance regimes, particularly fire and flooding (Busch & Smith 1995, Pettit & Naiman 2007). These patterns have been observed worldwide, although most studies focus on the moist temperate regions of Europe and North America (Cordes *et al.* 1997, Hupp & Osterkamp 1996, Naiman *et al.* 2005, Tabacchi *et al.* 1998); arid, semi-arid and subtropical regions of Europe, Africa, Australia and south-western North America (Bendix 1994a, Busch & Smith 1995, Friedman *et al.* 2006, Harris 1988, Hughes 1988, Hupp & Osterkamp 1996, Pettit *et al.* 2001, Tabacchi *et al.* 1996, Van Coller *et al.* 1997), or the moist tropics of South America (Junk 1999, Mertes *et al.* 1995, Salo *et al.* 1986). Longitudinal studies of the riparian vegetation in the Earth's largest biome, the tropical savannas, has been largely overlooked.

Bendix (1994b) proposed that the scale and strength of transverse (across channel) and longitudinal (parallel to channel) stream processes can be inferred from the composition of riparian vegetation. Bendix (1994a) predicted that where longitudinal processes operate hierarchically over a larger scale than transverse processes, vegetation will vary in distinct homogeneous zones moving from the headwaters to lower reaches.

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Conversely, domination by transverse processes will result in the formation of narrow bands of distinct vegetation running parallel to the watercourse, but homogeneous across the watershed. Generally, where processes operate hierarchically over multiple scales, the relative strength of transverse and longitudinal processes as well as the scale at which various processes operate can be inferred from the resulting patterns of vegetation.

In this paper we investigate vegetation patterns within a tropical river system that spans four geomorphologically distinct zones (constrained upland, braided valley, and unconstrained lowland and floodplain regions) that vary in the strength of the link between transverse and longitudinal processes. In zones where longitudinal processes predominate we predict that stream order will correlate strongly with vegetation, and vegetation composition will vary longitudinally but not transversely. Where the transverse dimension is strongly linked to stream processes we expect vegetation patterns to correlate with transverse variables (e.g. transverse profile and distance to main channel), and for distinct transverse bands of vegetation to co-vary along a gradient from headwaters to floodplain.

Our study site is located within the South Alligator River system in Kakadu National Park (KNP), a World Heritage site situated within the mesic tropical savanna zone of Northern Australia. The South Alligator River drains a relatively undisturbed 9000-km^2 catchment almost entirely contained within the boundaries of KNP. To our knowledge, this is the first comprehensive longitudinal study of vegetation patterns in a mesic (>1200 mm mean annual rainfall) tropical savanna river system.

METHODS

Study area

The riparian communities of Kakadu National Park exist amongst annual disturbance cycles of flood and fire. Rainfall is highly seasonal – over 90% of the 1100–1500 mm mean annual rainfall falls between November and March and water levels commonly exceed stream bank height (Finlayson 2005). Riparian vegetation exists within a matrix of savanna dominated by *Eucalyptus miniata* and *E. tetrodonta* (Wilson *et al.* 1991). The 1–2-m-high grass layer cures in the dry season and can then carry surface fires that burn 50% of the landscape annually (Russell-Smith *et al.* 1997).

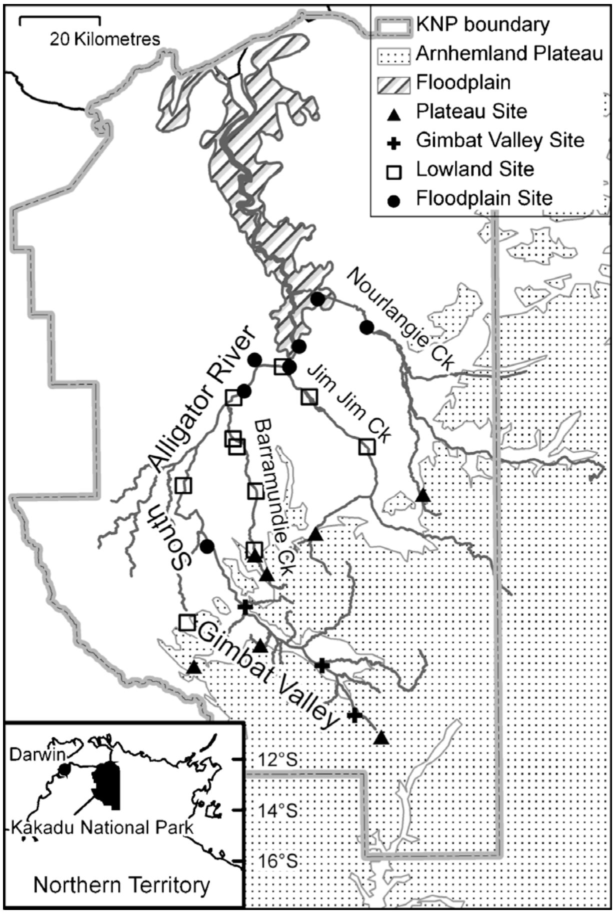

Figure 1. Map of the South Alligator River catchment and study locations.

The flora of the region lies along a moisture and topographic gradient that varies with dry-season access to the water table and the depth and length of wet-season inundation (Bowman & McDonough 1991, Finlayson 2005), although soil (Bowman & Dunlop 1986, Franklin *et al.* 2007) and fire (Russell-Smith *et al.* 2003) also contribute significantly to the complex patchwork of ecological communities. Broadly speaking, the hydrological gradient extends from low-lying annually submerged floodplains, then intermittently flooded woodlands, and finally more elevated woodlands that are not inundated.

The South Alligator River catchment is oriented along a south–north elevational gradient that crosses three land-system types: the Arnhem Land Plateau, the Gimbat Valley and the lowland plains (Figures 1 and 2). These elements are analogous to the erosional, transitional and depositional river provinces described by Tabacchi *et al.* (1998) but with two important qualifiers: (1) the gradient across the Arnhem Land Plateau is slight compared to the headwaters of the river systems described by Tabacchi *et al.* (1998) and the rate of upland erosion is extremely low (Saynor & Erskine 2006); (2) most deposition comes from downstream (via tidal influx, which extends 105 km inland; Woodroffe *et al.* 1989), rather than from upstream sources.

The headwaters of the South Alligator River are located on the Arnhem Land Plateau, a mass of uplifted

Figure 2. Photographs illustrating stretches of the South Alligator River catchment within each of four regions where vegetation was sampled, including a tributary within a ravine of the Arnhem Land Plateau, with forest dominated by *Melaleuca leucadendra* and *Xanthostemon eucalyptoides* (a); a depositional stretch containing sand bars in the Gimbat Valley with numerous *Melaleuca leucadendra* saplings growing along the sandbar and more developed riparian forest in the background (b); a typical section of the South Alligator River in the lowland plains with large *Melaleuca argentea* and *M. leucadendra* trees intermixed with *Barringtonia acutangula* abundant along the stream edge (c); and a perennial backwater lagoon (billabong) fringed with *Melaleuca viridiflora* that connects to the South Alligator River in the wet season (d).

Proterozoic sandstone lying 150–250 m above the surrounding lowlands (Figures 1 and 2a). Soils are generally veneers of sand seldom more than 150 mm thick (Russell-Smith *et al.* 1995). Creeks are typically confined within very narrow channels bounded by steep, sometimes vertical, sandstone banks. The porous sandstone also supports a large aquifer and numerous fissures produce springs that maintain dry-season flow within the major channel of the South Alligator River and some tributaries. However, most of the lower-order streams in the catchment are seasonal and cease flowing during the dry season.

The South Alligator River descends from the Plateau into the Gimbat Valley, a large valley running roughly south-east–north-west (Figures 1, 2b). Stream structure within the Gimbat Valley is often braided and complex with alternating depositional and erosional reaches. Step-pools are more abundant in the upper reaches in the valley, and pool-riffle-bar structures (Church 2002) are common in the lower reaches. Much of the watercourse is constrained to alluvial channels by vegetated sandy ridges (Wende & Nanson 1998).

After the Gimbat Valley the river crosses into large undulating lowland plains with highly eroded and laterized soils. Flow is constrained by a deeply incised channel bounded with alluvial ridges that are regularly breached in the wet season (Figures 1 and 2c). Some 120 km from the coast, the river joins two major tributaries, Jim Jim and Barramundie creeks, and the active river channel increasingly interconnects with a series of palaeochannels and cracking-clay floodplains that fill during the wet season and remain underwater for a substantial portion of the year (typically 4–7 mo; Finlayson 2005) (Figure 1d). Below its confluence with Jim Jim Creek, the active river channel drains into a vast floodplain. A tidal channel reforms some 10 km downstream but most wet-season flow is carried as surface flow across floodplains that reach up to 20 km wide.

Riparian-zone community structure

We surveyed 28 sites (Figure 1) along either active channels of the South Alligator River and its tributaries or backwater depressions on floodplains that connect to the South Alligator River in the wet season and retain water throughout the dry season (perennial billabongs). Surveys were conducted from April to September in 2003 and 2004. Sites were selected on the basis of interviews with both Aboriginal residents and Park staff to reflect a representative sample of communities throughout the Arnhem Land Plateau, Gimbat Valley and lowlands.

Within each site we established four to six transects of 200 m length, each running parallel to the main direction of the channel. We typically ran three transects on each side of a channel although if the opposite bank was inaccessible we established an additional three transects 1–2 km along the stream from the initial transects. Two transects were established within riparian forest that was >10 m wide, one adjacent to the main water-bearing channel and the second at a distance marking the midpoint of the forest community. In forests narrower than 10 m (22 out of 59) only one transect was used, and placed within the midpoint of the forest community. At all sites an additional transect was placed within the mid-point of the woodland community adjacent to the riparian forest (or 50 m from the forest boundary if the width of the woodland community was >200 m and hence immeasurable in the field).

At the site of each set of transects we recorded the widths of the riparian forest and woodland communities, the distance to the opposite bank of the water-bearing channel, the bank slope, the slope of the riparian forest and woodland communities (measured orthogonally to the active channel), and the aspect of the active channel. Where we were unable to calculate the riparian woodland distance in the field, we estimated the distance from 1:25 000 aerial photos taken in 2004. Woodland distances were positively skewed and were logarithmically transformed to approximate normality. A-horizon soil type was determined at each transect using the ribbon test of McDonald *et al.* (1998) and then classified into five textural groups: clay, clay-loam, loam, sand-loam and sand.

We recorded the species, diameter at breast height (dbh), and distance of the four closest trees >5 cm dbh along each transect at 20-m intervals (the point-centre-quarter method; Mueller-Dombois & Ellenberg 1974). For multi-stemmed trees, individual stems were recorded and basal area summed. Each tree was also scored for the presence or absence of charring on the trunk. At each 20-m interval we also recorded canopy cover using a densitometer, and scored each interval as burnt or unburnt. Strahler stream order (Strahler 1952) of the channel associated with each transect was calculated from 1:100 000 topographic mapsheets covering the South Alligator catchment (Royal Australian Survey Corps 1997).

Data analysis

Nomenclature, species groups and classification of transects. Nomenclature follows Kerrigan & Albrecht (2007). Some species shared highly similar functional attributes with other species and/or were difficult to distinguish in the field. These were aggregated as follows and treated as unique species for the purposes of community analysis: *Acacia* spp. – *Acacia aulacocarpa*, *Acacia difficilis*, *A. gonocarpa*, *A. hemignosta*, *A. holosericea*, *A. lacertensis*, *A. mountfordae*, *A. plectocarpa*, *A. sericoflora*, *A. torulosa*, *A. tropica*; *Calytrix* spp. – *Calytrix arborescens*, *C. brownii*; *Corymbia* spp. – *Corymbia foelscheana*, *C. latifolia*; *Ficus* spp. – *Ficus brachypoda*, *F. coronulata*, *F. racemosa*, *F. virens*; *Ficus aculeata/scobina* – *Ficus aculeata*, *F. scobina*; *Gardenia* spp. – *Gardenia fucata*, *G. kakaduensis*; *Pavetta* spp. – *Pavetta brownii*, *Pavetta* sp.

Each transect was attributed based on (1) vegetation structure (riparian closed-forest and woodland) and (2) region (Plateau, Gimbat Valley, lowland). To test for transverse variation in riparian closed-forests, transects occurring within the forest were further classified by whether they were closest to the watercourse (‘stream’) or in the middle of the riparian zone (‘middle’). Where there was only one forest transect it was attributed as ‘stream’. All transects within sites at backwater depressions were simply classified as ‘floodplain’ without further classification as all occurred in the lowlands and were typically surrounded by homogeneous vegetation without a distinct fringe around the billabong.

Multivariate analyses. We used two techniques to test for differences in community composition across transverse and longitudinal gradients: (1) Ordination using non-metric multidimensional scaling (NMDS) with the packages MASS 7.2–29 and Vegan 1.8–5 in R 2.4.0 (http://cran.r-project.org). Bray–Curtis dissimilarity was calculated between the fourth-root-transformed dominance scores within each transect. (2) The percentage of similarity between each transect class (stream, middle, savanna and floodplain) and the contribution of each taxon to the overall similarity between classes was quantified by the SIMPER routine in PRIMER (Version 6.1.2, Plymouth Marine Labs, Plymouth, UK; Clarke & Warwick 1994). These differences were statistically tested using one-way analysis of similarities (ANOSIM) to non-parametrically test the average rank similarities of samples between classes.

To test for correlation between dominant vegetation and other environmental variables we first divided the environmental data set into two groups: (1) Soil type: a categorical environmental variable. (2) Width of the riparian woodland and forest zones; distance to the opposite bank; slope of the bank, riparian forest zone and riparian woodland zone; channel aspect; stream order; per cent of trees charred and per cent of quadrats burnt. These continuous environmental variables were normalized so that comparisons between variables of different scales and origins were meaningful. This was achieved by subtracting from the mean and dividing by the standard deviation for each variable, giving each variable the same mean (0) and variance (1).

Environmental variables were selected that maximized the rank correlation between a similarity matrix of the variable set and the transformed dominant vegetation scores (the BEST procedure in PRIMER 6.1.2). Subset similarity matrices of taxa that contributed >10% to total dominance in any transect were also correlated with the overall vegetation matrix to determine the subset of taxa that best explained the variation between communities. Soil was fitted to the MDS ordination scores as a generalized additive model (GAM) using the R package vegan.

The BEST procedure is considered more robust than other methods that typically rely on linear regression (Clarke & Ainsworth 1993). However, it is difficult to visually interpret. We decided to use BEST to select the most important variables and then present those variables here as linearly correlated vectors. This is useful for interpretation, but can be misleading when it masks non-linear patterns. To avoid misinterpretation we also separately plotted each variable as a fitted two-dimensional GAM surface. Where there were significant deviations from the linear pattern implied by fitted vectors we discuss them in the explanatory text with each figure.

RESULTS

Dominant vegetation structure

A total of 125 woody species >5 cm dbh were recorded, including species that were later aggregated into groups for analysis (see Appendix 1 for a complete list of species recorded). The SIMPER-derived measurement of similarity within transect groups was very low, indicating a high degree of diversity between sites (the most similar group, floodplains, had a within-group similarity of only 30%, Table 1). Moreover, despite a very clear structural distinction between forest, woodland and floodplain vegetation communities, there was intergradation of taxa between community types, and most transect groups shared about 10% of their species with other groups. There was no distinguishable difference between the dominant taxa of stream and middle transects within riparian forest.

Table 1. Per cent similarity of mature woody species between and within groups (within-group similarities are indicated by bold). Parentheses indicate the level of difference between groups using the ANOSIM non-parametric test statistic R in Primer 6.1.2 (0 indicates complete similarity, 1 indicates complete dissimilarity). The significance of R against the null hypothesis of no difference (R = 0) is indicated by an asterisk (P < 0.001).

	Floodplain	Woodland	Middle	Stream
Floodplain	**29.9**			
Woodland	9.0 (0.55*)	**19.7**		
Middle	9.2 (0.61*)	12.2 (0.37*)	**23.9**	
Stream	10.0 (0.63*)	9.0 (0.58*)	25.2 (0.04)	**26.7**

Table 2. Fire history and cover by transect type. 'Quadrats burnt' indicates the mean percentage of quadrats scored as burnt during field surveys. 'Trees charred' indicates the mean percentage of trees with indications of charring scored during field surveys. The standard error is provided after the mean.

Transect type	% Cover	% Quadrats burnt	% Trees charred
Floodplain	52.6 ± 7.0	11.2 ± 6.0	30.2 ± 8.3
Closed-forest – stream	77.9 ± 3.6	2.6 ± 2.4	25.6 ± 6.4
Closed-forest – middle	73.4 ± 5.5	3.7 ± 3.7	30.9 ± 9.1
Woodland	38.9 ± 4.5	44.5 ± 8.0	72.3 ± 7.2

Table 3. Transverse stream profiles and dominant species richness by region. All slopes are perpendicular to the main direction of the channel. The standard error is provided after the mean.

Region	Woodland slope (%)	Forest slope (%)	Bank slope (%)	Forest width (m)
Plateau	8.1 ± 1.6	5.6 ± 1.1	31.3 ± 2.9	59.3 ± 31.9
Gimbat Valley	8.3 ± 1.9	5.4 ± 1.1	24.8 ± 1.7	25.7 ± 3.9
Lowland	1.0 ± 0.4	9.1 ± 1.5	33.3 ± 1.7	30.7 ± 2.6
Floodplain	0.5 ± 0.4	2.1 ± 0.5	20.8 ± 2.8	28.7 ± 4.0

Forest and woodland vegetation segregated by cover and the occurrence of fires, as well as floristic composition (Table 2, Figure 3; see Appendix 2). Soil texture segregated with community type along both longitudinal and transverse axes: woodlands were typically found on sandy loams or sands, riparian communities on sand, and floodplains on clay and clay loams (Figure 4).

The transverse profile of streams differed amongst regions (Table 3). Bank slope was relatively similar across regions, but this was an inadequate indication of the transverse profile. Floodplain banks often had a very slight profile (on the order of 10 cm), whereas lowland banks along the main channel of the South Alligator River were

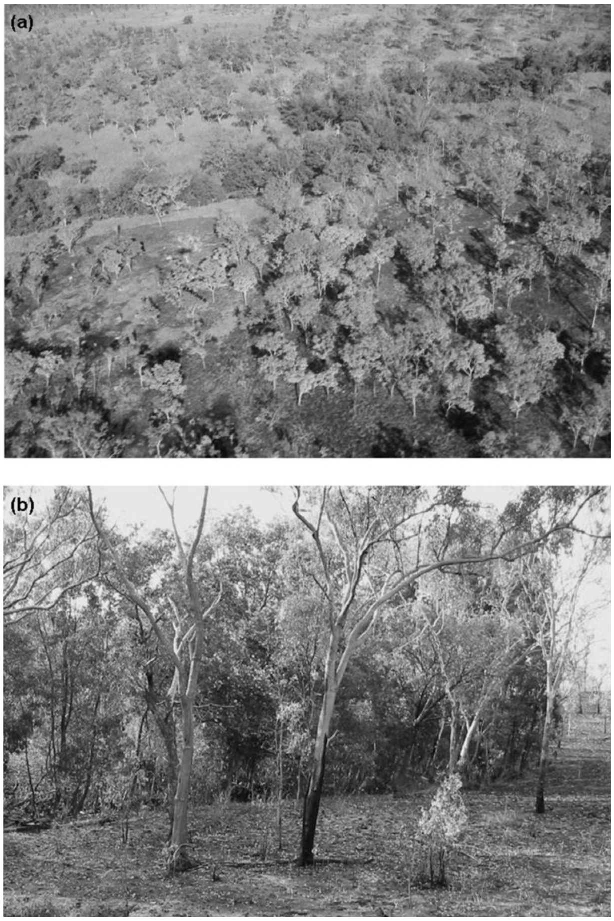

Figure 3. Fire along the woodland–closed-forest boundary. An aerial view of Gerowie Creek, a small tributary of the South Alligator River. A fire through upland and riparian woodland in the foreground stopped short of the darker band of closed-forest following the creek horizontally across the upper third of the photo (a). The adjoining riparian woodland in the background is unburnt. A fire along a different section of Gerowie Creek stopped after burning into the edge of the riparian forest (b).

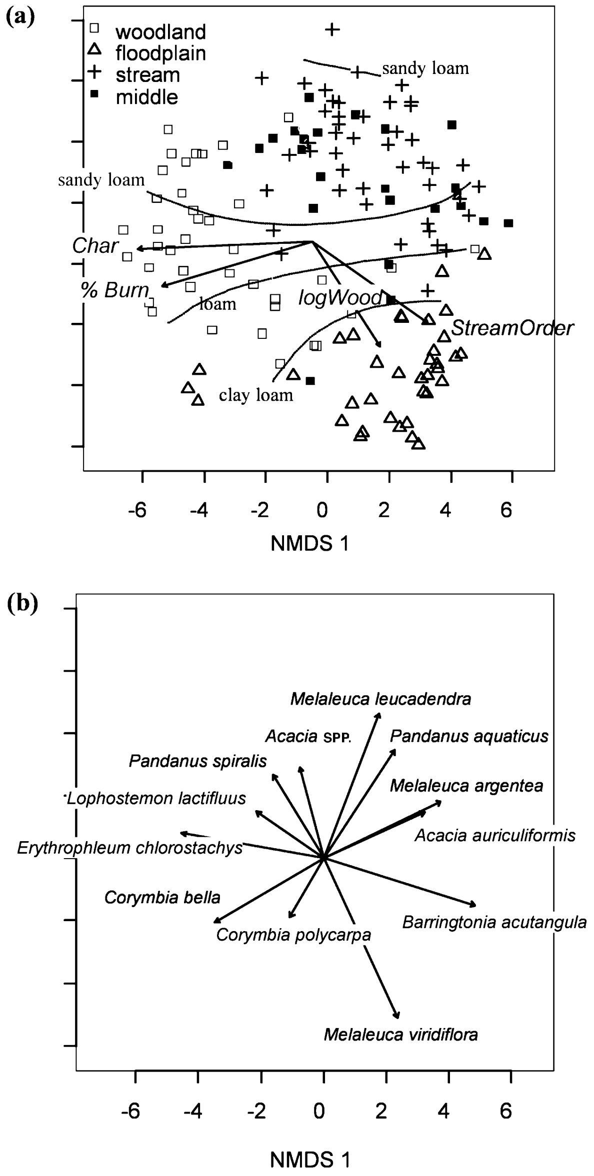

Figure 4. NMDS ordination of all transects (N = 144, stress = 24.5). A best-fit of environmental vectors provided a Pearson's correlation of $\rho = 0.42$ from four variables: stream order, the logarithmic distance of the riparian woodland zone (logWood), percentage of trees charred (Char) and percentage of quadrats burned (PctBurn) (a). Also shown is a GAM fit of soil type. A vector fit of 11 species provided a Pearson's correlation of $\rho = 0.90$ (b). *Lophostemon lactifluus* and *Pandanus spiralis* do not follow the gradient indicated by their vectors but their greatest abundances are centred on the tip of their respective vectors, and generally decline away from that point.

frequently 5–10 m high. A better indicator of vertical relief was the slope within the forest vegetation zone, which typically abutted the dry-season watercourse and rarely extended more than 10 m beyond the channel bank. Average slope within forest vegetation was similar between the Plateau and Gimbat Valley, and then increased dramatically in the lowland plains. By contrast, the average slope of the adjacent woodland vegetation declined, and the width of the woodland vegetation zone increased, an overall indication of the increased extent of the seasonal inundation zone in the lowlands. Closed-forests along the more developed banks of lowland plains did not differ in width from their upstream counterparts.

The species composition of riparian closed-forests was largely independent of the transverse profile, and varied with stream order (Figure 5). Forests were generally dominated by *Melaleuca leucadendra* in the Plateau and Gimbat Valleys and co-dominated by *Melaleuca argentea* and *M. leucadendra* along lowland forests. Plateau riparian forest sites were more likely than other regions to contain species otherwise associated with woodland (*Lophostemon lactifluus*, *Grevillea pteridifolia*, *Erythrophleum chlorostachys* and *Corymbia ptychocarpa*,

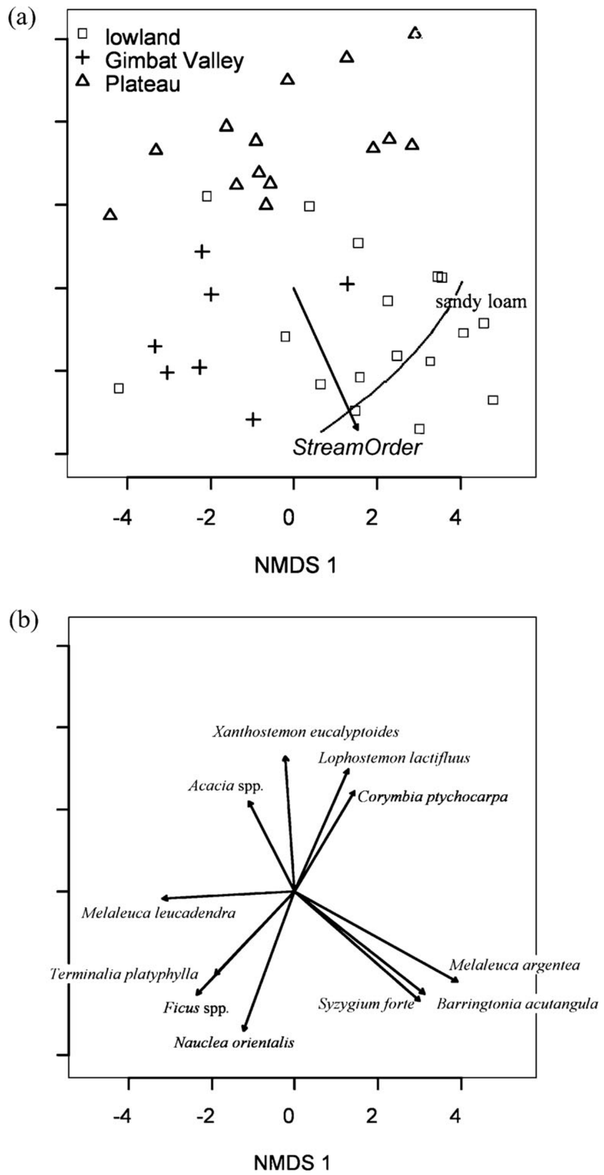

Figure 5. NMDS ordination of riparian transects (N = 39, stress = 17.2). Basal area scores of stream and central transects were combined within each site. Data points are displayed according to biogeographic region. A best-fit of environmental vectors provided a Pearson's correlation of $\rho = 0.45$ from one variable, stream order (a). Also shown is a GAM-fit of soil type. A vector fit of 11 species provided a Pearson's correlation of $\rho = 0.75$ (b). The gradient of *Melaleuca leucadendra* does not follow the gradient indicate by its vector, but is most abundant towards the centre-left of the ordination and declines away from that position.

Figure 5b). Two riparian-forest sites were floristically distinct from each other and all other sites and contained neither *Melaleuca* spp. nor species associated with woodland or floodplain sites. These are indicative of the highly diverse, but relatively small, pockets of non-*Melaleuca*-dominated closed forest that line streams in monsoonal north Australia.

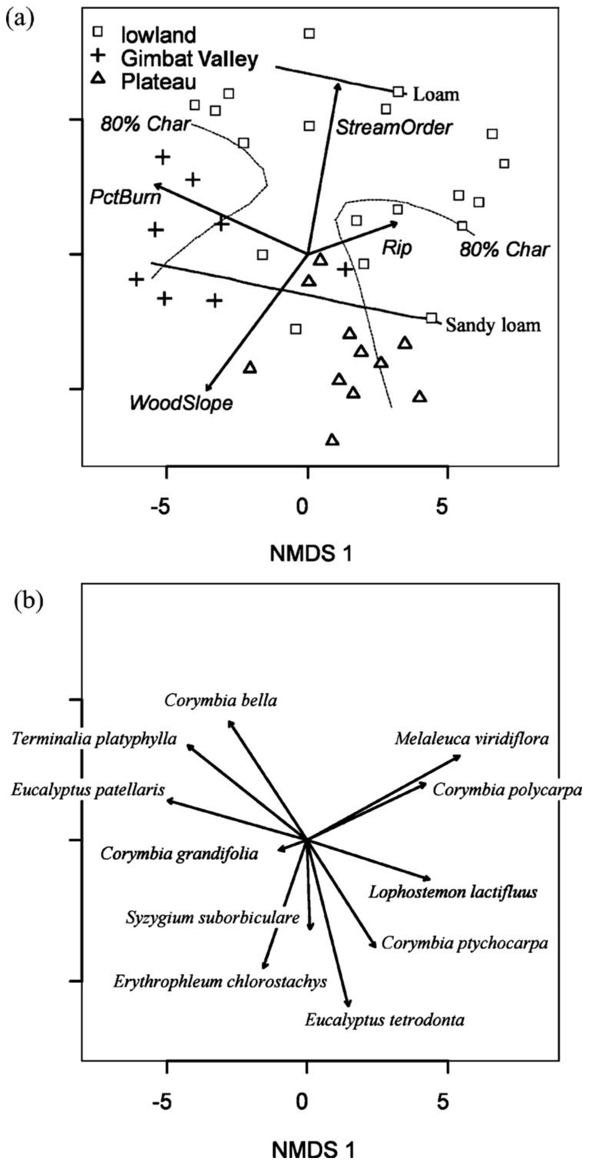

Figure 6. NMDS ordination of woodland transects (N = 38, stress = 21.9). Data points are displayed according to biogeographic region. A best-fit of environmental vectors provided a Pearson's correlation of $\rho = 0.41$ from six variables: stream order, width of the riparian forest zone (Rip), percentage of quadrats burnt (PctBurn), percentage of trees charred (Char) and slope within the riparian woodland zone (WoodSlope) (a). Also shown is a GAM fit of soil type. The gradient of riparian width is non-linear, with higher values trending towards the upper right and lower centre of the ordination. Char is also non-linear, and the GAM contour line representing 80% of trees charred is shown in place of a vector to avoid misinterpretation. A vector fit of eleven species provided a Pearson's correlation of $\rho = 0.91$ (b). The gradient of *Erythrophleum chlorostachys* is non-linear with the greatest abundance tending toward the centre of the vector.

The composition of open woodland varied greatly. Stream order and woodland slope were negatively correlated (Figure 6) such that high-order lowland streams often had low woodland profiles, and hence were particularly susceptible to flooding. Low-order streams on the Plateau were frequently abutted by *Eucalyptus tetrodonta* woodlands (Figure 6b), the dominant upland plant community in the region. *Syzygium suborbiculare, Erythrophleum chlorostachys* and other upland taxa were also more common within woodlands on high slopes. *Corymbia bella, C. ptychocarpa, C. polycarpa, C. grandifolia* and *Lophostemon lactifluus* occupied lower positions. At the lowest point of the topographic gradient, *Melaleuca viridiflora* commonly occupied poorly drained depressions within lowland woodlands.

The composition of floodplain vegetation along backwater depressions varied according to stream order, with little transverse zonation. Dense *Melaleuca viridiflora* and *M. cajuputi* forests tended to dominate closed-forests along depressions connected to high-order streams while sparse *Vitex glabrata* and *Corymbia bella* open-woodlands were associated with lower-order streams.

Fire

Fire occurrence was strongly associated with woodland communities and within woodland communities formed an orthogonal axis to slope (Figure 6a). Judging from the occurrence of burnt quadrats and charred trees, fire occurrence is relatively rare within riparian forests (Table 2). The percentage of charred trees in woodlands was generally very high (>60%) and was not correlated with other fire indicators. Rather sites split bimodally into one group positively correlated with frequent fires and another negatively correlated (Figure 6a). Woodland communities in the Plateau were the least burnt amongst woodlands, possibly reflecting topographic protection. In woodland sites overall, species found along high-order streams and low slopes were associated with lower fire frequencies. Likewise, floodplains associated with lower-order streams had a higher fire frequency than high-order floodplains.

DISCUSSION

We observed variation in riparian vegetation across three different directions and scales: transversely across the woodland/forest boundary, longitudinally within the forest community, and longitudinally within the woodland community. The boundary between woodland and forest riparian communities was structurally distinct and persisted from the headwaters to the lower reaches, only breaking down in the floodplains. This implies large-scale control by transverse processes across most of the catchment. At a smaller scale, forest vegetation segregated into distinct communities based on longitudinal position, and stream order was the strongest correlate of community composition (Figure 5), implying strong dominance by longitudinal processes within riparian forests. Finally, woodland communities varied either independently or dependently of longitudinal variables depending on the strength of the transverse connection between woodland and stream.

We propose that the woodland forest boundary is formed by declining dry-season access to groundwater away from the active channel and the impact of regular fires carried from woodland towards the water channel that limit the recruitment of forest species within the woodland zone, and this has been observed in comparable river systems in Australia and elsewhere. Lamontagne *et al.* (2005) indicated that dry-season access to water was the most important factor in the establishment of closed-forest vegetation along the Daly River, a larger river system 300 km to the south-east of the South Alligator River. Groundwater access has also been linked to vegetation distribution in arid and semi-arid river systems (Hupp & Osterkamp 1996, Van Coller *et al.* 1997).

The nearly universal dominance of *Melaleuca* along streams in this study contrasts a study by Douglas *et al.* (2003) of small intermittent streams along lower reaches of the South Alligator River. There, streamside vegetation primarily comprised woodland species (e.g. *Erythrophleum chlorostachys*, *Corymbia polycarpa*, *Lophostemon lactifluus*, *Melaleuca nervosa*, *M. viridiflora* and *Terminalia platyphylla*) and had lower cover than that reported for riparian forests here. Our study did not include smaller intermittent streams, and taken together both studies suggest that a minimum level of stream size is needed to form *Melaleuca* closed-forest. Both *M. leucadendra* and *M. argentea* are relatively fire-tolerant (Franklin *et al.* 2007) and may establish the closed canopy under which other, less fire-tolerant vegetation can develop; both species are absent from the riparian vegetation described by Douglas *et al.* (2003). Once a closed *Melaleuca* canopy establishes, higher humidity and lower grass cover inhibit the incursion of fires into the closed-forest zone (Pettit & Naiman 2007), and may encourage the establishment of fire-intolerant species. Indeed, species elsewhere associated with closed-forest, fire-intolerant 'rain-forest' communities (as described by Russell-Smith 1991) were common within most *Melaleuca*-dominated riparian forests. In Plateau regions, topographic protection from fire may also explain why the riparian forest is wider on average than for other regions, despite smaller stream sizes (Table 3).

Longitudinal variation within riparian closed-forest communities may be the result of increased scouring or depth and duration of flooding at lower reaches. However, the increased topological complexity of stream channels in lower reaches (Table 3) would suggest that there should be greater transverse differentiation in lower reaches than in upper reaches. Franklin & Bowman (2004) find evidence of topographic differentiation along high-profile streams that support bamboo, but our own results indicate that transverse differentiation of other species is not pronounced.

Alternatively, longitudinal variation in riparian forest may be due to vicariance in species distributions or to edaphic changes across regions that were undetected by this study. Some evidence for vicariance is given by the close affinity between the geographic location of non-*Melaleuca* riparian forest species within this study and rain-forest species of similar geographic provenance (Russell-Smith 1991), regardless of their affinity for moist or dry soils.

The transverse profile of woodland sites co-varied with region, with higher woodland slopes found on sites in the Gimbat Valley and the Plateau than on the lowlands. Fire frequency was strongly correlated with Gimbat Valley sites and less so with Plateau sites, and varied orthogonally to stream order. There was a higher abundance of upland savanna species within both Gimbat Valley and Plateau sites than in lowland sites. This indicates weak transverse linkages between stream processes and adjacent woodland communities in the Gimbat Valley and Plateau, and suggests that differences in vegetation composition between these two regions are due more to fire frequency than hydrology. The close affinity between the vegetation of lowland woodland sites and floodplain sites, both of which predominantly have low slopes and lie along high-order streams, suggests that transverse linkages between stream processes (i.e. flooding) and woodland communities are much stronger in the lowlands. Interestingly, those lowland woodland communities adjacent to wider riparian forests also had a higher abundance of *Melaleuca viridiflora* which is strongly associated with floodplain communities (Appendix 2).

The development from headwaters to coastal plain of stronger transverse linkages between vegetation and stream processes fits patterns described for large floodplain systems in the Amazon basin (Junk 1999, Mertes *et al.* 1995, Salo *et al.* 1986) and the south-eastern USA (Hupp 2000). These studies all demonstrate a tight linkage between stream processes and vegetation and conclude that riparian vegetation composition is a function of length of inundation and geomorphological structure. However, in these regions riparian closed-forest is extensive and rainfall more consistent throughout the year than in our study region. Studies of xeric savanna systems in Africa (Hughes 1988, Pettit & Naiman 2007, Van Coller *et al.* 1997), mesic savanna systems in South America (Kellman *et al.* 1998) and arid systems in the south-western USA (Busch 1995) are also consistent with this study and others (Dwire & Kauffman 2003, Pettit & Naiman 2007) in finding that upland processes, particularly fire, can be as significant as hydrology and geomorphology in structuring streamside vegetation.

Although the potential exists for a comprehensive linkage of upland, riparian and fluvial processes into one coherent theory of riverine structure and function (Poole 2002), there have been few attempts to directly link riparian vegetation models with models developed for fluvial processes such as nutrient transfer, productivity and aquatic patterns of biodiversity. However, the similarities between the interaction of longitudinal and transverse processes within riparian communities described here and similar interactions in fluvial systems are telling. For example, the river continuum concept (Vannote *et al.* 1980) postulated that river processes vary continuously along a gradient from headwaters to floodplain. This was later refined to a 'patchy' gradient or 'discontinua' (Townsend 1989). Later observations of large tropical rivers and unmodified temperate rivers prompted the development of the flood-pulse concept (Junk 1999) to explain temporal and transverse variation in rivers subjected to repeated flooding. Recent models (Poole 2002, Thorp *et al.* 2006) combine both flood-pulse and discontinua models where the strength of the connections between hydrological and geomorphological processes at different scales determines which ecological processes apply in particular zones. Thus, along the unconstrained lowland reaches of a large river where there are strong transverse linkages between systems, the flood-pulse concept may adequately describe observed ecological patterns, however upstream where channels are geomorphologically constrained and longitudinal processes predominate, the river continuum concept may apply (Poole 2002).

We have demonstrated a pattern of variation in vegetation across scales and directions in a large mesic savanna river system. At the largest scale, the opposing processes of fire and groundwater delineate a sharp transverse boundary between woodland and forest. At a smaller scale, variation in hydrology and geomorphological constraint create a gradient in transverse linkages between stream processes and riparian vegetation. Transverse linkages are relatively weak in the Plateau and the Gimbat valley, and variation in riparian forest may be described as a patchy longitudinal gradient between plateau and valley flora. In the lowlands, transverse links are stronger due to low relief and an annual pulse of floodwater that increases with stream order. It would be of interest to test whether in-stream patterns of diversity, nutrient availability and productivity vary similarly to the variation in vegetation across regions.

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Appendix 1. List of all woody species > 5 cm dbh recorded. The number of records and mean basal area (m^2 ha^{-1}) are also provided. Nomenclature follows Kerrigan & Albrecht (2007).

Species	Family	No. records	Mean BA (m^2 ha^{-1})
Acacia aulacocarpa	Mimosaceae	4	0.009
Acacia auriculiformis	Mimosaceae	132	0.037
Acacia difficilis	Mimosaceae	38	0.009
Acacia gonocarpa	Mimosaceae	2	0.003
Acacia hemignosta	Mimosaceae	1	0.003
Acacia holosericea	Mimosaceae	34	0.029
Acacia lacertensis	Mimosaceae	17	0.006
Acacia lamprocarpa	Mimosaceae	4	0.009
Acacia mountfordae	Mimosaceae	1	0.032
Acacia plectocarpa	Mimosaceae	14	0.006
Acacia sericoflora	Mimosaceae	2	0.016
Acacia sp.	Mimosaceae	2	0.011
Acacia torulosa	Mimosaceae	51	0.009
Acacia tropica	Mimosaceae	37	0.006
Adenia sp.	Passifloraceae	1	0.003
Allosyncarpia ternata	Myrtaceae	39	0.144
Alphitonia sp.	Rhamnaceae	26	0.012
Alstonia actinophylla	Apocynaceae	6	0.203
Antidesma ghaesembilia	Euphorbiaceae	28	0.010
Asteromyrtus symphyocarpa	Myrtaceae	82	0.021
Barringtonia acutangula	Lecythidaceae	392	0.047
Bauhinia malabarica	Caesalpiniaceae	2	0.013
Brachychiton diversifolius	Sterculiaceae	8	0.030
Brachychiton megaphyllus	Sterculiaceae	1	0.008
Brachychiton paradoxus	Sterculiaceae	3	0.005
Breynia cernua	Euphorbiaceae	3	0.017
Bridelia tomentosa	Euphorbiaceae	12	0.005
Buchanania arborescens	Anacardiaceae	11	0.034
Buchanania obovata	Anacardiaceae	33	0.016
Calophyllum sil	Clusiaceae	1	0.020
Calytrix arborescens	Myrtaceae	3	0.014
Calytrix brownii	Myrtaceae	3	0.004
Canarium australianum	Burseraceae	15	0.014
Carallia brachiata	Rhizophoraceae	59	0.020
Cathormion umbellatum	Mimosaceae	322	0.030
Cochlospermom fraseri	Bixaceae	1	0.007
Corymbia bella	Myrtaceae	260	0.058
Corymbia bleeseri	Myrtaceae	2	0.048
Corymbia confertiflora	Myrtaceae	4	0.018
Corymbia disjuncta	Myrtaceae	14	0.043
Corymbia foelscheana	Myrtaceae	16	0.037
Corymbia grandifolia	Myrtaceae	39	0.034
Corymbia latifolia	Myrtaceae	13	0.054
Corymbia polycarpa	Myrtaceae	97	0.075
Corymbia polysciada	Myrtaceae	22	0.034
Corymbia porrecta	Myrtaceae	2	0.009
Corymbia ptychocarpa	Myrtaceae	139	0.033
Cyclophyllum schultzii	Rubiaceae	22	0.006
Denhamia obscura	Celastraceae	2	0.012
Diospyros calycantha	Ebenaceae	3	0.071
Diospyros humilis	Ebenaceae	1	0.003
Drypetes deplanchei	Euphorbiaceae	10	0.011
Elaeocarpus arnhemicus	Eleaocarpaceae	20	0.009
Erythrina vespertilio	Fabaceae	1	0.006
Erythrophleum chlorostachys	Caesalpiniaceae	165	0.044
Eucalyptus alba	Myrtaceae	8	0.064
Eucalyptus bigalerita	Myrtaceae	20	0.098
Eucalyptus miniata	Myrtaceae	32	0.067
Eucalyptus patellaris	Myrtaceae	81	0.069
Eucalyptus tectifica	Myrtaceae	3	0.006
Eucalyptus tetrodonta	Myrtaceae	68	0.063
Eucalyptus tintinnans	Myrtaceae	12	0.090

Appendix 1. Continued.

Species	Family	No. records	Mean BA (m^2 ha^{-1})
Ficus brachypoda	Moraceae	6	0.490
Ficus coronulata	Moraceae	8	0.126
Ficus opposita	Moraceae	15	0.017
Ficus racemosa	Moraceae	16	0.252
Ficus scobina	Moraceae	23	0.008
Ficus virens	Moraceae	2	1.090
Gardenia fucata	Rubiaceae	4	0.006
Gardenia kakaduensis	Rubiaceae	1	0.003
Glochidion apodogynum	Euphorbiaceae	25	0.013
Gmelina schlechteri	Verbenaceae	3	0.005
Grevillea decurrens	Proteaceae	1	0.002
Grevillea pteridifolia	Proteaceae	71	0.008
Gymnanthera oblonga	Asclepiadaceae	2	0.007
Hakea arborescens	Proteaceae	6	0.007
Helicia australasica	Proteaceae	10	0.004
Ilex arnhemensis	Aquifoliaceae	2	0.019
Livistona benthamii	Arecaceae	10	0.045
Livistona humilis	Arecaceae	1	0.013
Lophopetalum arnhemicum	Celastraceae	4	0.013
Lophostemon grandiflorus	Myrtaceae	33	0.103
Lophostemon lactifluus	Myrtaceae	183	0.069
Maranthes corymbosa	Chrysobalanaceae	16	0.037
Melaleuca argentea	Myrtaceae	260	0.205
Melaleuca cajuputi	Myrtaceae	83	0.074
Melaleuca dealbata	Myrtaceae	45	0.044
Melaleuca leucadendra	Myrtaceae	478	0.173
Melaleuca nervosa	Myrtaceae	33	0.022
Melaleuca viridiflora	Myrtaceae	667	0.051
Melicope elleryana	Rutaceae	15	0.018
Nauclea orientalis	Rubiaceae	59	0.145
Notelaea microcarpa	Oleaceae	3	0.028
Owenia vernicosa	Meliaceae	11	0.084
Pandanus aquaticus	Pandanaceae	211	0.013
Pandanus spiralis	Pandanaceae	129	0.020
Pavetta brownii	Rubiaceae	1	0.005
Pavetta sp.	Rubiaceae	1	0.004
Persoonia falcata	Proteaceae	3	0.008
Petalostigma pubescens	Euphorbiaceae	15	0.009
Petalostigma quadriloculare	Euphorbiaceae	2	0.005
Phyllanthus reticulatus	Euphorbiaceae	5	0.007
Planchonia careya	Lecythidaceae	34	0.008
Polyalthia australis	Annonaceae	2	0.009
Sesbania formosa	Fabaceae	19	0.047
Strychnos lucida	Loganiaceae	71	0.015
Syzygium angophoroides	Myrtaceae	1	0.008
Syzygium armstrongii	Myrtaceae	172	0.077
Syzygium eucalyptoides	Myrtaceae	8	0.021
Syzygium forte	Myrtaceae	115	0.136
Syzygium minutuliflorum	Myrtaceae	17	0.043
Syzygium nervosum	Myrtaceae	11	0.011
Syzygium suborbiculare	Myrtaceae	66	0.063
Terminalia carpentariae	Combretaceae	27	0.011
Terminalia erythrocarpa	Combretaceae	31	0.014
Terminalia ferdinandiana	Combretaceae	11	0.005
Terminalia grandiflora	Combretaceae	18	0.021
Terminalia microcarpa	Combretaceae	42	0.010
Terminalia platyphylla	Combretaceae	95	0.047
Timonius timon	Rubiaceae	26	0.009
Vavaea australiana	Meliaceae	2	0.008
Vitex acuminata	Verbenaceae	3	0.005
Vitex glabrata	Verbenaceae	37	0.034
Wrightia pubescens	Apocynaceae	1	0.004
Xanthostemon eucalyptoides	Myrtaceae	170	0.045
Xanthostemon paradoxus	Myrtaceae	15	0.019

Appendix 2. The contribution of each taxon to similarity within each vegetation community. Some species were grouped (see methods for details). Average basal area (m^2 ha^{-1}), average within-group similarity, the ratio of mean similarity to standard deviation, the contribution of each taxa to total within-group similarity, and the cumulative per cent contribution are shown for each taxa. Deciduousness and the ability to resprout after fire are derived from the Tropical Savannas Fire Response Database (http://www.landmanager.org.au/view/index.aspx?id=327234). Nomenclature follows Kerrigan & Albrecht (2007).

	Basal area (m^2 ha^{-1})	Average Similarity	Ratio of Similarity:SD	Cumulative% contribution to group similarity	Deciduous	Resprout
Riparian forest taxa						
Melaleuca leucadendra (Myrtaceae)	0.37	5.63	0.83	19.1	–	+
Pandanus aquaticus (Pandanaceae)	0.20	3.96	1.33	32.6	–	+
Melaleuca argentea (Myrtaceae)	0.31	3.76	0.67	45.3	–	+
Syzygium armstrongii (Myrtaceae)	0.21	2.43	0.65	53.6	–	+
Barringtonia acutangula (Lecythidaceae)	0.16	1.46	0.45	58.6	+	+
Pandanus spiralis (Pandanaceae)	0.13	1.33	0.55	63.1	–	+
Acacia auriculiformis (Mimosaceae)	0.13	1.13	0.45	66.9	–	–
Lophostemon lactifluus (Myrtaceae)	0.13	1.06	0.42	70.5	–	+
Acacia spp. (Mimosaceae)	0.11	1.01	0.46	74.0	– (generally)	– (generally)
Syzygium forte (Myrtaceae)	0.15	0.91	0.31	77.0	–	+
Xanthostemon eucalyptoides (Myrtaceae)	0.13	0.87	0.33	80.0	–	+
Melaleuca viridiflora (Myrtaceae)	0.11	0.87	0.37	82.9	–	+
Nauclea orientalis (Rubiaceae)	0.11	0.68	0.31	85.2	+	+
Grevillea pteridifolia (Proteaceae)	0.07	0.57	0.36	87.2	–	+
Carallia brachiata (Rhizophoraceae)	0.09	0.55	0.39	89.1	–	+
Ficus spp. (Moraceae)	0.10	0.45	0.22	90.6	–	mixed
Riparian woodland taxa						
Erythrophleum chlorostachys (Caesalpiniaceae)	0.17	2.85	0.64	14.2	+	+
Corymbia bella (Myrtaceae)	0.14	2.41	0.46	26.2	–	+
Syzygium suborbiculare (Myrtaceae)	0.12	1.73	0.49	34.9	–	+
Lophostemon lactifluus (Myrtaceae)	0.13	1.62	0.44	42.9	–	+
Corymbia polycarpa (Myrtaceae)	0.11	1.09	0.34	48.3	–	+
Melaleuca viridiflora (Myrtaceae)	0.10	1.00	0.30	53.3	–	+
Corymbia ptychocarpa (Myrtaceae)	0.09	0.99	0.34	58.2	–	+
Pandanus spiralis (Pandanaceae)	0.08	0.97	0.44	63.1	–	+
Eucalyptus tetrodonta (Myrtaceae)	0.10	0.76	0.28	66.9	–	+
Eucalyptus patellaris (Myrtaceae)	0.08	0.61	0.21	69.9	–	+
Ficus aculeata/scobina (Moraceae)	0.05	0.50	0.31	72.4	–	+
Acacia spp. (Mimosaceae)	0.05	0.50	0.31	74.9	– (generally)	– (generally)
Buchanania obovata (Anacardiaceae)	0.06	0.49	0.28	77.3	–	+
Corymbia grandifolia (Myrtaceae)	0.06	0.46	0.27	79.6	–	+
Terminalia platyphylla (Combretaceae)	0.05	0.45	0.22	81.9	+	+
Corymbia latifolia/foelscheana (Myrtaceae)	0.06	0.37	0.22	83.7	–	+
Barringtonia acutangula (Lecythidaceae)	0.05	0.28	0.20	85.1	+	+
Eucalyptus bigalerita (Myrtaceae)	0.05	0.25	0.16	86.3	–	+
Vitex glabrata (Verbenaceae)	0.04	0.25	0.18	87.6	+	+
Terminalia grandiflora (Combretaceae)	0.04	0.24	0.20	88.8	+	+
Eucalyptus miniata (Myrtaceae)	0.05	0.24	0.17	90.0	–	+
Planchonia careya (Lecythidaceae)	0.03	0.21	0.20	91.0	–	+
Floodplain taxa						
Melaleuca viridiflora (Myrtaceae)	0.35	14.22	1.20	49.3	–	+
Barringtonia acutangula (Lecythidaceae)	0.20	5.56	0.65	68.6	+	+
Cathormion umbellatum (Mimosaceae)	0.19	4.51	0.50	84.2	+	+
Melaleuca cajuputi (Myrtaceae)	0.09	0.99	0.27	87.7	–	+
Corymbia bella (Myrtaceae)	0.06	0.63	0.19	89.8	–	+
Acacia auriculiformis (Mimosaceae)	0.06	0.54	0.26	91.7	–	–