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Niche differentiation and regeneration in the seasonally flooded *Melaleuca* forests of northern Australia

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Abstract: Gallery and floodplain forests in monsoonal northern Australia are mostly sclerophyllous and dominated by five closely related species of *Melaleuca* (Myrtaceae) amongst which niche differentiation is unclear. We present a floristic and environmental analysis of 'the flooded forest' using data from 340 plots distributed across 450 000 km^2 of the Top End of the Northern Territory. *Melaleuca argentea* was confined to streams and occurred on sandier substrates, whereas *M. cajuputi* mostly occurred in the near-coastal lowlands on clay soils. The greater basal area of *M. cajuputi* suggests an association with productive sites. *Melaleuca dealbata*, *M. viridiflora* and *M. leucadendra* occurred on a wide range of soils. More deeply floodprone sites were occupied by *M. argentea* and *M. leucadendra* along streams and by *M. leucadendra* and *M. cajuputi* on floodplains and in swamps. A general deficiency but occasional abundance of *Melaleuca* seedlings suggests that regeneration is episodic. Seedlings were more frequent in recently burnt areas and especially where fires had been severe. We propose that *Melaleuca* forests occur where disturbance by fire and/or floodwater is too great for rain forest to persist, rendering them the wetland analogue to the eucalypts that dominate well-drained portions of the north Australian environment.

Key Words: disturbance, episodic regeneration, fire, flood, floodplain forest, gallery forest, niche differentiation, paperbark forests, rain forest, soils

INTRODUCTION

In all but the most arid of tropical regions, riverine (gallery) and floodplain forests are usually evergreen or semi-deciduous mesophyllous closed forests (Kellman *et al.* 1998, Richards 1981, Sarmiento & Pinillos 2001). This holds true even where drainage is poor or inundation prolonged (Ferreira 2000, Parodi & Freitas 1990). However, in northern Australia mesophyllous gallery forests are the exception, with riverine and floodplain-fringe environments frequently dominated by sclerophyllous evergreens in the genus *Melaleuca* (paperbarks, Myrtaceae) that form floristically simple woodlands or open forests (Fox *et al.* 2001, Wilson *et al.* 1990). Bowman *et al.* (1993) suggested that *Melaleuca* replaces rain forest in the presence of frequent fire; indeed the botanical name *Melaleuca* refers to the black and white pattern on the trunks caused by the shedding of fire-blackened thick papery bark. However, this relationship is not well established: Williams (1984) attributed declines in *Melaleuca* to high fire frequencies, and Franklin & Bowman (2004) noted that *Melaleuca* gallery forests occupied fire-sheltered positions downslope from fire-sensitive monsoonal vine-thickets.

The genus *Melaleuca* contains 227 species, of which 219 occur in Australia (Craven & Lepschi 1999). The *M. leucadendra* complex of 10 species ('broad-leaved paperbarks') dominates tropical and sub-tropical wetlands (Blake 1968, Craven & Lepschi 1999). Gallery and floodplain *Melaleuca* forests of the Top End of the Northern Territory (hereafter, 'the flooded forest') feature five members of the complex, *M. argentea* W. Fitzg., *M. cajuputi* Powell, *M. dealbata* S.T. Blake, *M. leucadendra* (L.) L. and *M. viridiflora* Sol. ex Gaertn. (Cowie *et al.* 2000, Finlayson 2005, Finlayson & Woodroffe 1996). A sixth species of the complex, *M. nervosa* (Lindl.) Cheel occurs sympatrically on poorly drained sites inundated for only a short period each year (Briggs 1981, Finlayson & Woodroffe 1996). A seventh member of the complex, *Melaleuca quinquenervia* (Cav.) S. T. Blake, occupies

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wetlands in eastern Australia and some Pacific Islands and is a serious invasive species of wetlands in Florida, Puerto Rico and Hawaii (Pratt *et al.* 2005, Serbesoff-King 2003, Turner *et al.* 1997).

Of the coastal floodplains of the Top End, Cowie *et al.* (2000) noted 'There is little correspondence between the presence of *Melaleuca* trees and the composition of the understorey' and that differences between dominant species cannot be readily explained in terms of geomorphology. In their regional descriptions of vegetation, Wilson *et al.* (1990) and Fox *et al.* (2001) recognized only a generic '*Melaleuca* forest (Paperbark Swamp)' map unit, whilst gallery paperbark forests receive scant mention and no formal classification. Briggs (1981) and Finlayson & Woodroffe (1996) suggested a role for differences in the length of time inundated in discriminating coastal floodplain species, whilst Bowman *et al.* (1993) emphasized the role of landscape setting in discriminating three species in an upland setting.

Melaleuca communities are sensitive to a range of environmental disturbances including saltwater intrusion, increased or decreased fire frequencies and heavy grazing (Crowley & Garnett 1998, Edwards *et al.* 2003, Sharp & Bowman 2004, Williams 1984, Winn *et al.* 2006). One of the aims of this study is to provide context for a programme investigating vegetation change in the floodprone forests of Kakadu National Park, a World Heritage-listed reserve covering 20 000 km^2 in the Top End. A more general aim is to provide a floristic and environmental overview of a neglected but widespread and ecologically important vegetation type in northern Australia. To this end, we analyse floristic and environmental data from 340 flooded forest sites distributed across a 450 000 km^2 area embracing all of the Top End of the Northern Territory, and stand structure data collected at a sub-set of 117 of these sites. Our questions in these analyses are three-fold: (1) At the landscape scale, how do the *Melaleuca* spp. of the flooded forest partition the environment? (2) In what environmental settings and amongst which *Melaleuca* spp. do rain-forest plant associates occur? (3) Is regeneration in the flooded forest continuous or driven by disturbance? Collectively, this information provides a basis for understanding why the Australian tropical savanna landscape lacks typical mesophytic gallery forests.

STUDY AREA

Melaleuca-dominated forests and woodlands are a feature of wooded floodplains and gallery forests in the Northern Territory north of *c.* 18° South – the Top End (Figure 1). The region's climate is monsoonal, characterized by warm to hot temperatures throughout the year and rainfall that is almost entirely confined to the Austral summer months of October to April (Cook & Heerdegen 2001, McDonald & McAlpine 1991). Mean annual rainfall varies from 500 mm in the south to 1800 mm in the north, and features fewer rain days per unit rainfall, and thus more rainfall per rain day than other tropical regions (Jackson 1988).

Given the intense seasonality of rainfall, river and wetland levels fluctuate markedly (Sandercock & Wyrwoll 2005) and in a manner that is highly predictable among though not within seasons. There are few data about the time that *Melaleuca* forests and woodlands remain inundated. Franklin & Bowman (2003) analysed 27 y of gauge data from the upper tidal section of the Adelaide River and found that *Melaleuca leucadendra* dominated the lower portion of the riparian forest where the ground was inundated every year and for a median period of 56 d including a median of 37 consecutive days. Finlayson & Woodroffe (1996) noted that on floodplains, *M. leucadendra* open woodland can remain under water for more than 6 mo.

In the study area, the soils of floodplains and embedded swamps along with lentic (major) watercourses are mostly Quaternary alluvium of loam to clay texture, tending to sandy in the vicinity of sandstone and granite outcrops. A range of other parent materials occur on lotic (minor) streams and as residual outcrops elsewhere. Many rivers have extensive coastal floodplains of Holocene origin which are close to or even below sea-level and protected from salt-water inflow by cheniers – coralline sand ridges imposed on swampland by cyclonic wave action (Mulrennan & Woodroffe 1998, Nott 2006). The vegetation of floodplains consists of grasslands and sedgelands fringed with floodplain forests of *Melaleuca* and sometimes rain forest (Bowman & McDonough 1991, Finlayson & Woodroffe 1996).

METHODS

Data collection

Data were collected from July to November 1993 at 340 sites across the Top End selected to represent the geographic, floristic and structural range of the vegetation communities of which *Melaleuca* is a feature. Additional data on size class distributions were collected at 117 sites. The latter sites were selected for what was then perceived to be their forestry potential, and thus feature larger trees and greater predominance of *Melaleuca* in the canopy.

At each site, a 20 × 20-m plot was established, the location of which was identified using a GPS. From the centre of the plot, a Bitterlich gauge sweep was used to estimate basal area of the stand and each of its component species. The following were also recorded: the identity

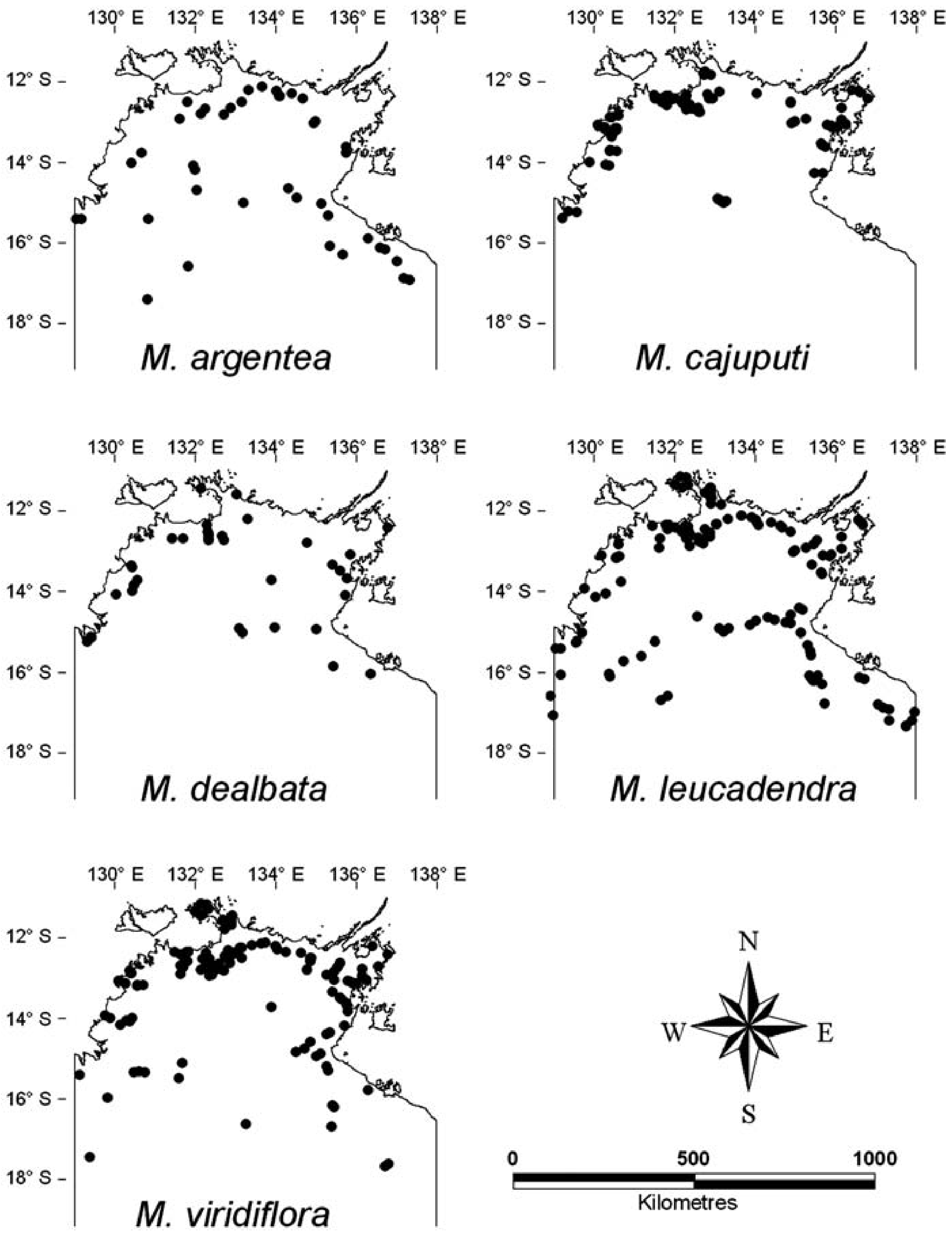

Figure 1. Distribution of five *Melaleuca* species in the Top End of the Northern Territory, Australia as recorded in 340 flooded forest plots.

of all mid-storey and ground-layer species present along with an estimate of the projective foliage cover of each; parent material; soil texture in classes of sand, sandy loam, loam, clay loam and clay (McDonald *et al.* 1990); landform element following McDonald *et al.* (1990); slope measured in degrees with a clinometer; an estimate of the surface cover of gravel and rock; the height above ground of the flood mark; and evidence of fire in five classes (no evidence, some trees scorched, most trees scorched, some trees killed, most trees killed).

All *Melaleuca* plants in 200-m (sometimes 100- or 150-m) transects 10 m in width were counted and attributed to 5 cm diameter size classes (at 1.3 m height). Plants were classified as seedlings and counted separately if they were less than 50 cm tall.

Analyses

A classification of the sites based on the basal area of species from the Bitterlich gauge sweeps was performed in PC-Ord 4.32 using the Bray–Curtis distance measure and flexible UPGMA. The 30 species present at six or more sites were included, along with three pseudospecies formed by summing the basal area of species recorded at less than six sites into vegetation classes (rain forest, savanna, riparian forests) based on their habitat preference (Brock 2001, Russell-Smith & Dunlop 1987).

Generalized linear models were generated for the following response variables: (1) The presence/absence of rain-forest species in any stratum in the 20 × 20-m plots. Rain-forest species were as defined by Russell-Smith & Dunlop (1987). The model was binomial with a logit link function. Explanatory variables considered were: landscape ‘setting’, geology, soil texture, mean annual ‘rainfall’, elevation, slope, and rock cover. (2) The dominant species of *Melaleuca*, based on the basal area sweep. The few cases where two species had identical basal area were randomly allocated to one or the other. The model was multinomial with a logit link function. Explanatory variables considered were as for model (1). (3) The density of seedlings. Seedling densities had a severely skewed distribution with numerous zero values: they were $\log_{10}(x+2)$-transformed, the purpose of the +2 addition being to ensure that no zero values remained. The transformed variables were modelled with a gamma distribution and log link function, the resulting *P*-plot of residuals proving to be surprisingly acceptable. Explanatory variables considered were: fire, soil texture and the basal area of *Melaleuca* plants other than seedlings.

Explanatory variables were generated and/or interpreted for analysis as follows. Elevation was determined from topographic maps and log(x+1)-transformed. Mean annual rainfall was identified for each site using the BIOCLIM module of ANUCLIM 5.1. Slope was log(x+1) transformed. ‘Rock cover’ is the combined cover of gravel and rock as recorded in the field. Five landscape settings were generated from the landform elements recorded in the field by pooling as follows: stream = bank, channel bench, levee, stream bank or stream channel; swamp = drainage depression, oxbow or swamp (run-on settings); floodplain = backplain, flood-out, plain, swale or valley flat (flat environments); tidal = inter-tidal flat or supra-tidal flat; and hill = footslope, hillcrest or hillslope. Summary data are presented for all five settings, but tidal and hill sites were excluded from models due to the small sample size. Geological settings were aggregated from field data into two states: Quaternary sediments and other. Fire state was aggregated into three classes: no evidence, some trees scorched, and other classes combined. Rock cover was log(x+1)-transformed.

From the above it follows that elevation, rainfall, slope, rock cover and basal area are continuous variables, whereas setting, geology and fire state are categoric variables. Soil texture was alternately considered as a categoric or continuous variable.

Generalized linear modelling was performed in Statistica 7.0. Only first-order effects were considered. All subset models were ranked using the Akaike Information Criterion (AIC_C, Burnham & Anderson 2002), in which lower values of AIC_C indicate greater support. Only well-supported models ($\Delta i < 2.0$, i.e. those for which AIC_C was no more than 2.0 greater than the model with the most support) that generally explained more than 20% of the deviance were further evaluated.

RESULTS

Floristic patterns and environmental partitioning

All flooded forest *Melaleuca* species were widespread in the study area with the qualification that *M. cajuputi* was confined to the northern lowlands and one cluster of sites inland on the Roper River (Figure 1).

Sixty-two per cent of sites had one species of *Melaleuca*, 35% had two species and 3% had three species. All possible pair-wise combinations of the five species were observed except *M. argentea* with *M. dealbata*, the only strong pattern of co-occurrence being that of *M. leucadendra* at sites dominated by *M. argentea* (Table 1). A classification of sites failed to yield convincing floristic subdivisions because monodominant stands of each species were comprehensively linked by gradients of mixed species-stands.

As measured by Bitterlich gauge sweeps, stand basal area in the flooded forest varied from 0.75 to 52.0 $\text{m}^2\ \text{ha}^{-1}$, and of the *Melaleuca* species within it from 0.5 to 52.0 $\text{m}^2\ \text{ha}^{-1}$. *Melaleuca* basal area differed significantly amongst the dominant species (ln(x+1)-transformed; $F_{4,335} = 4.00$, $P = 0.004$), the higher basal area of *M. cajuputi*-dominated stands differing significantly from those of *M. argentea* and *M. viridiflora* (Tukey's HSD, $P < 0.05$) (Figure 2a).

Well-supported multinomial models for environmental partitioning amongst stands dominated by each of the five flooded-forest *Melaleuca* species consistently contained landscape setting and elevation as the major effects (Table 2). There was strong support for the addition of a geological variable (model 2), which was, however, substituted by soil texture treated as a continuous variable in model 3. These may be interpreted as follows (Table 3, Figure 2b,c): *Melaleuca argentea* is confined to streams

Table 1. Matrix of association among the flooded forest *Melaleuca* species in the Top End of the Northern Territory; n = 340 sites. Secondary species are expressed as a proportion of sites occupied by the primary species. Tertiary species, of which there were few, have been ignored. Proportions in bold are monospecific stands.

	Dominant *Melaleuca* species				
Secondary *Melaleuca* species	*M. argentea* (n = 30)	*M. cajuputi* (n = 80)	*M. dealbata* (n = 32)	*M. leucadendra* (n = 103)	*M. viridiflora* (n = 95)
M. argentea	**0.467**	0.013	0	0.087	0
M. cajuputi	0	**0.613**	0.094	0.087	0.116
M. dealbata	0	0	**0.594**	0	0.042
M. leucadendra	0.467	0.125	0.031	**0.612**	0.074
M. viridiflora	0.067	0.225	0.156	0.204	**0.684**
other	0	0.025	0.125	0.010	0.084

Table 2. Well-supported multinomial generalized linear models of environmental partitioning amongst five species of *Melaleuca* in the flooded forests of the Top End of the Northern Territory; n = 309 sites. Variables are listed in descending order of contribution to the per cent of deviance explained (%DE) within each model. (c) = categoric variable.

Model	AIC_C	Δi	%DE
1. setting (c), elevation	777.59	0	19.2
2. setting (c), elevation, geology (c)	778.71	1.12	20.0
3. setting (c), elevation, soil texture	779.26	1.67	20.0

Table 3. Landscape settings for the five species of the flooded forest expressed as % occurrence. Landscape settings are based on pooled landform elements. Sites are attributed to the *Melaleuca* species with the highest basal area. 'Tidal' and 'hill' sites were not included in the multinomial modelling (Table 2).

	% frequency					
Species	tidal	floodplain	swamp	stream	hill	n
M. argentea	0	0	0	100	0	29
M. cajuputi	0	32	53	12	4	78
M. dealbata	0	26	55	10	10	31
M. leucadendra	1	11	30	58	0	100
M. viridiflora	1	33	53	10	3	94

Table 4. Variation with landscape setting and *Melaleuca* species in floodmark heights (m) in the flooded forests of northern Australia.

	Stream		Floodplain/swamp	
Species	median	n	median	n
M. argentea	2.0	29	–	0
M. cajuputi	1.0	9	0.5	65
M. dealbata	0.5	3	0.05	25
M. leucadendra	1.5	58	0.5	41
M. viridiflora	0.4	9	0.1	81

and occurs on sandier substrates; *M. cajuputi* is largely confined to the lowlands, particularly floodplains and swamps, and often occurs on clay soils; *M. dealbata* and *M. viridiflora* were more frequent on floodplains and swamps and *M. leucadendra* along streams, the latter three species occurring across a wide range of elevation and soil textures.

The height of flood marks varied between landscape settings (Mann–Whitney $U = 5666$, $P < 0.0000001$), being greater along streams (median = 1.45 m, range 0–13 m) than floodplains or swamps (median = 0.3 m, range 0–5 m). Along both streams and floodplains and swamps, the height of flood marks varied with dominant species (streams: Kruskal–Wallis $H_{4,108} = 11.0$, $P = 0.027$; floodplains and swamps: Kruskal–Wallis $H_{3,212} = 30.3$, $P < 0.0001$). Along streams, the two primary stream species (*M. argentea* and *M. leucadendra*) had higher flood marks (Table 4) but there was no significant difference between them (Mann–Whitney $U = 716$, $P = 0.26$). On both streams and floodplains and swamps, *M. viridiflora* and *M. dealbata* had markedly lower flood marks than other species (Table 4).

Melaleuca and rain-forest plants

One or more monsoon rain-forest plant species were recorded in 52.1% of flooded-forest plots. Their occurrence differed significantly among dominant *Melaleuca* species ($\chi^2 = 42.9$, df = 4, $P << 0.001$), being greatest in association with *M. argentea* (93.1% of plots), moderate with *M. leucadendra* (65.0%) and relatively low in *M. dealbata*, *M. cajuputi* and *M. viridiflora* (43.8, 41.0 and 34.7% respectively). Models of environmental correlates were unconvincing. However, the occurrence of monsoon rain-forest plants varied significantly amongst the three landscape settings ($\chi^2 = 53.2$, df = 2, $P << 0.001$), being greatest along streams (80.8%) and much lower on floodplains (40.3%) and swamps (35.3%).

Regeneration

The frequency profile of *Melaleuca* stem sizes did not conform to the reverse-J profile characteristic of continually regenerating forests for any of the dominant *Melaleuca* species (Figure 3). Twenty-one of 117 transects

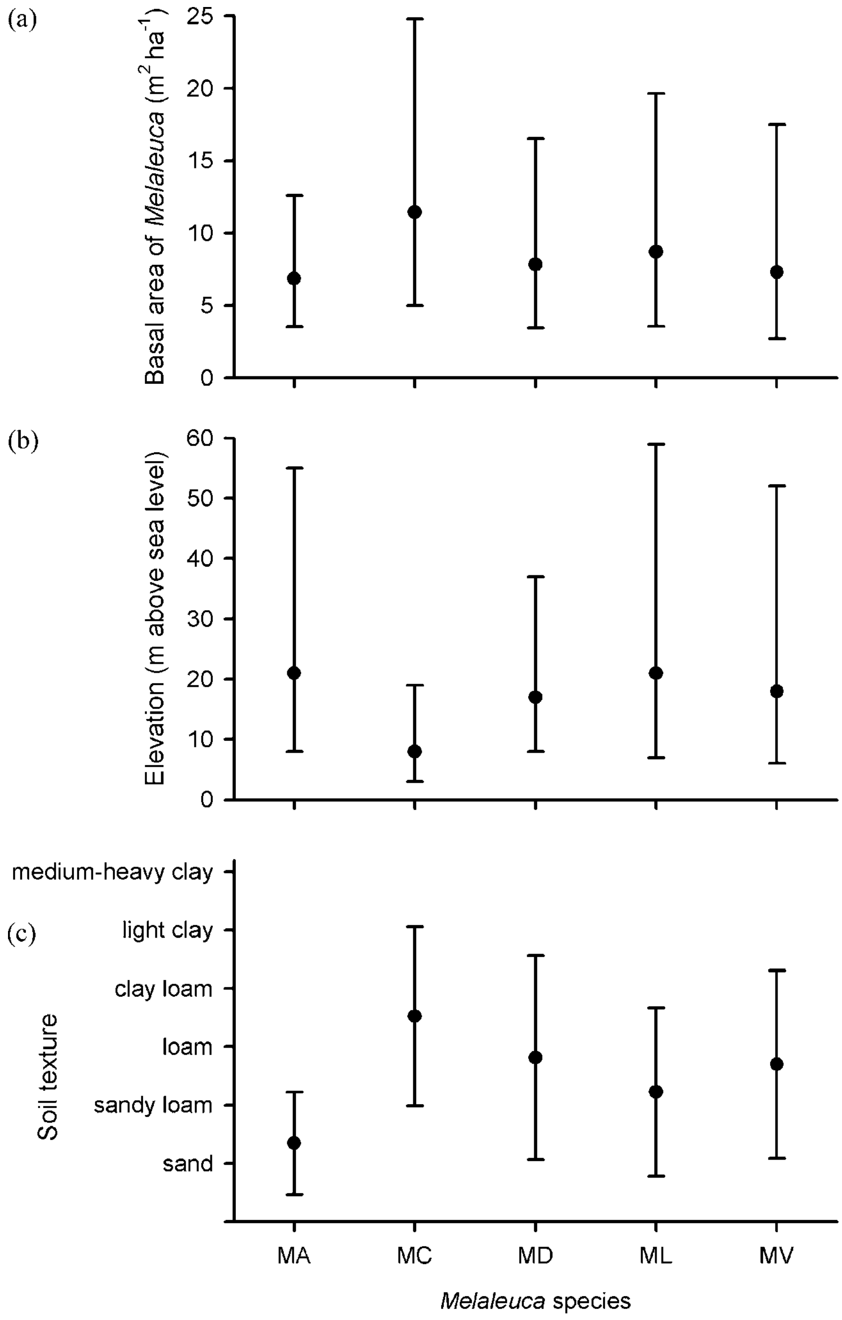

Figure 2. Basal area (a), elevation (b) and soil texture (c) profiles (mean ± SD) for the five flooded forest *Melaleuca* species in the Top End of the Northern Territory. MA = *M. argentea*; MC = *M. cajuputi*; MD = *M. dealbata*; ML = *M. leucadendra*; MV = *M. viridiflora*. Basal area and elevation have been back-transformed. Soil texture has been treated as a continuous variable.

(17.9%) had no stems under 5 cm in diameter and 65 transects (55.6%) had no seedlings.

The two well-supported models for the density of seedlings both included effects of fire and soil texture (Table 5). Seedling density increased with an increase in the severity of recent fires (Figure 4a), and was markedly higher on loam than other soils (Figure 4b). A negative effect of the basal area of larger *Melaleuca* plants explained an additional 2.6% of the deviance (Table 5, Figure 4c).

DISCUSSION

Floristics and the environment

Of the five flooded forest *Melaleuca* species, *M. argentea* and *M. cajuputi* had the most identifiably discrete niches. *Melaleuca argentea* occupied sandy river banks, where it taps groundwater during the dry season (Lamontagne *et al.* 2005, O'Grady *et al.* 2006). In contrast, *M. cajuputi*

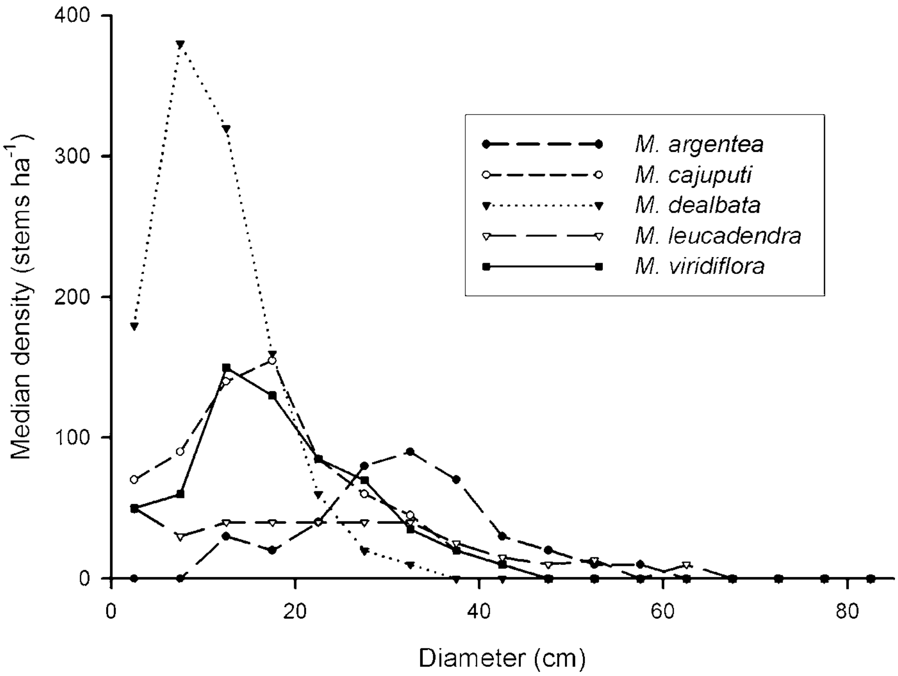

Figure 3. Variation amongst dominant *Melaleuca* species in the density of *Melaleuca* stems in 5-cm diameter classes.

Table 5. Well-supported generalized linear models of the relationship between environmental variables and the density of seedlings < 50 cm tall in flooded forests of the Top End of the Northern Territory; n = 111 sites. Variables are listed in descending order of contribution to the per cent of deviance explained (%DE) within each model. Basal area is of *Melaleuca* and for all size classes other than seedlings < 50 cm tall. (c) = categoric variable; (−) = a negative directional continuous effect.

Model	AIC$_C$	Δ*i*	%DE
1. fire (c), soil texture (c), basal area (−)	206.83	0	26.0
2. fire (c), soil texture (c)	208.77	1.94	23.4

was largely confined to heavier soils on deeply inundated coastal floodplains and swamps in the higher-rainfall north, where its high basal areas suggest remarkable productivity in the face of waterlogging, as is indeed the case (Kogawara *et al.* 2006, Yamanoshita *et al.* 2005). However, high tolerance of waterlogging may not in itself define the niche of *M. cajuputi* as *Melaleuca leucadendra* occupied similarly inundation-prone sites on floodplains and in swamps, and it and occasionally *M. viridiflora* are known to occur on fertile bottomlands prone to prolonged inundation (Bowman *et al.* 1993, Finlayson & Woodroffe 1996). Cowie *et al.* (2000) considered *M. leucadendra* to be the species most tolerant of waterlogging, this study indicating that the species has a broad niche. *Melaleuca dealbata* and *M. viridiflora* occupied sites that are less deeply floodprone but were largely confined to floodplains and swamps. Our finding for *M. viridiflora* is consistent with previous reports (Bowman *et al.* 1993, Briggs 1981, Finlayson & Woodroffe 1996), but there appear to be no previous reports concerning the niche of *M. dealbata*. More detailed examination of soil properties and how these interact with waterlogging may prove informative.

Notwithstanding the above, the only identifiable floristic patterns were a strong tendency of all species to form monospecific stands, and an association between *M. argentea* and *M. leucadendra* along streams. Combined with evidence of extensive overlap in a range of the niche dimensions considered here and as noted by Cowie *et al.* (2000), this raises the possibility that niches remain incompletely resolved. The coastal floodplains are of recent (mid-Holocene) origin (Mulrennan & Woodroffe 1998, Woodroffe *et al.* 1985) and it is plausible that current patterns of occupancy partly reflect lottery settlement events.

Disturbance, regeneration and rain forest

A key question in the ecology of the flooded forest is why it is so frequently dominated by sclerophyllous *Melaleuca* species instead of mesophyllous rain-forest trees. Several simple hypotheses may be rejected, at least in stand-alone form. The phenomenon is unlikely to be related to greater tolerance of waterlogging by *Melaleuca* because *Melaleuca* also frequently dominates sites subject to only brief inundation, and because some Top End rain-forest species thrive on sites subject to prolonged inundation. Examples of the latter include the swamp fan-palm *Livistona benthamii* F. M. Bailey and the tall rain-forest

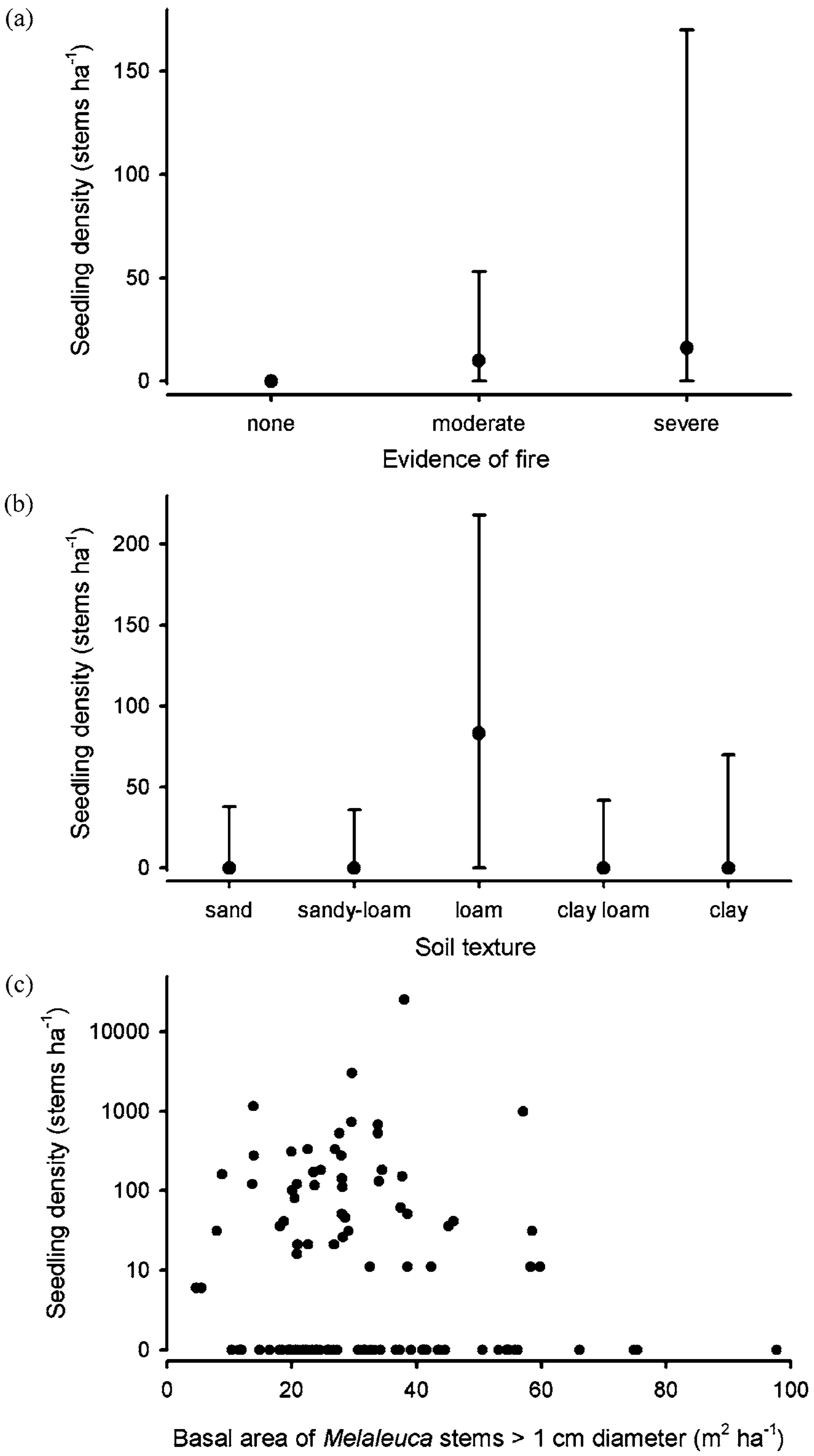

Figure 4. The relationship between seedling density and environmental variables identified as important by generalized linear modelling. Values in (a) and (b) are median and 25–75th percentiles. Evidence of fire classes (with the sample size) are: none = no evidence of fire (28); moderate = some trees fire-scarred (51); severe = all trees fire-scarred and/or in a few cases, some or all the trees killed by fire (32). Sample sizes for soil texture classes are 23, 15, 14, 30 and 29 respectively.

tree *Gmelina schlechteri* H. J. Lam (Bowman & McDonough 1991). Nor is it simply explicable in terms of the marked seasonal dryness of some floodprone sites, as a variety of seasonally dry sites in the Top End are occupied by semi-deciduous vine-thicket (Russell-Smith 1991) including the floodprone upper portion of river banks

(Franklin & Bowman 2004). The evident ability of some *Melaleuca* species to cope with extreme seasonal contrasts of waterlogging and drought may extend beyond the capability of most rain-forest species, but this could at most account for the dominance of *Melaleuca* at only a limited range of sites. The ability of *Melaleuca* to survive fire could explain why rain forest occurs upslope from *Melaleuca* forest on some floodplain fringes (Bowman & McDonough 1991) where fires burn in from floodplain grasslands during the dry season (Gill *et al.* 2000, Haynes 1985, Russell-Smith *et al.* 1997). But it cannot explain why *Melaleuca* forest frequently occurs downslope from semi-deciduous vine-thickets on river banks (Franklin & Bowman 2004), a situation where fires originate upslope in adjacent savannas.

We propose that *Melaleuca* is resilient to and favoured by disturbance particularly in the form of either, or both, fire and the erosive force of floodwaters along streams. We note that on spring-fed and often waterlogged sites in the Top End sheltered from both fire and erosive floodwaters, rain forest usually predominates (Bowman & Minchin 1987, Russell-Smith 1991). Disturbance by fire and flood are near-annual features of Top End riverine and floodplain systems (Franklin & Bowman 2003), though sites differ substantially in their exposure in a somewhat complementary manner. Thus, whilst floodplain forests are prone to the intrusion of fire from adjacent floodplain grasslands and savanna, major watercourses are often topographically sheltered from fire but frequently flooded and subject to significant erosion and channel change (Hancock & Evans 2006) following the intense and often cyclonic rainfall events that are a feature of the region (Jackson 1988). The erosive force of floodwaters is greatest on stream banks (Saynor & Erskine 2006) and can restrict regeneration to species with rapid root growth and small leaves (Gurnell 1997, Karrenberg *et al.* 2003).

Our observation that regeneration in the flooded forest *Melaleuca* species is episodic, as also noted for *M. cajuputi* by Bowman & Rainey (1996), and positively correlated with disturbance by fire, is consistent with this hypothesis. In *M. leucadendra* at least, there is no persistent seed bank, and germination may be enhanced by water-borne dispersal and subsequent lodgement in flood debris (Pettit & Froend 2001).

Evolution and biogeography

In being dominated by closely related myrtaceous species and in forming open forests and woodlands on a wide range of soils, the flooded forest constitutes a floodprone analogue to the eucalypt-dominated savannas of adjacent, better-drained sites. The diversification of *Melaleuca* and occupation of habitat normally occupied by gallery rain forest in northern Australia is consistent with a broader pattern in Australia in which late-Tertiary aridity and increasing frequency of landscape fire is thought to have caused the loss of rain forest and driven the sustained diversification of eucalypts (Bowman 2000, Martin 2006).

Faunal specialization also provides evidence that the *Melaleuca* forests developed over a long period of evolutionary time. In contrast to those of many rain-forest trees, *Melaleuca* fruits are dry capsules and the seeds are tiny, but the flowers are showy, heavily scented and produce an abundance of nectar (Franklin & Noske 2000, Woinarski *et al.* 2000*a*). As a consequence, *Melaleuca* communities support rich avifaunal communities dominated by nectarivorous birds and bats (Woinarski & Braithwaite 1993, Woinarski *et al.* 2000*b*), a vagile fauna that doubtless plays a critical role in the dispersal of pollen.

CONCLUSION

Northern Australia features notably intense rainfall events, a high frequency of tropical cyclones, and exceptionally high frequencies of fire. A prominent, positive role for disturbance from these sources in the ecology of the flooded forest *Melaleuca* species suggests superb adaptation to this capricious environment. An inherent 'weediness' may have implications for the invasiveness of the closely related and ecologically analogous *M. quinquenervia* of eastern Australia in tropical and subtropical wetlands in the Americas.

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