Drivers of rain-forest boundary dynamics in Kakadu National Park, northern Australia: a field assessment

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Abstract: Understanding the causes of savanna–forest dynamics is vital as small but widespread changes in the extent of tropical forests can have major impacts on global climate, biodiversity and human well-being. Comparison of aerial photographs for 50 rain-forest patches in Kakadu National Park had previously revealed a landscape-wide monotonic expansion of rain-forest boundaries between 1964 and 2004. Here floristic, structural, environmental and disturbance attributes of the changes were investigated by sampling 588 plots across 30 rain-forest patches. Areas that had changed from savanna to rain forest were associated with a significantly higher abundance of rain-forest trees and less grasses, relative to stable savanna areas. Ordination analyses showed that overall floristic composition was not significantly different between newly established rain forest and longer established rain forest. Generalized linear models also indicated that contemporary levels of disturbance (fire and feral animal impact) and environmental variables (slope and soil texture) were poor predictors of historical vegetation change. We concluded that (1) the rain-forest boundaries are highly dynamic at the decadal scale; (2) rain-forest expansion is consistent with having been driven by global environmental change phenomena such as increases in rainfall and atmospheric CO_2; and (3) expansion will continue if current climatic trends and management conditions persist.

Keywords: climate, fire ecology, global environmental change, tropical rain forest, vegetation dynamics

INTRODUCTION

Tropical forests cover only *c.* 10% of the land surface, but are of significant importance globally as they store and cycle large amounts of carbon in the atmosphere, contain more than 50% of the world's species, and in many cases directly sustain human livelihoods and culture (Groombridge & Jenkins 2003, Malhi & Grace 2000). Small changes in the extent of tropical forests can therefore have major impacts on climate, biodiversity and human well-being. Understanding the mechanisms of changes to tropical forests is particularly important in light of the risk of potentially dangerous positive feedbacks with the climate system that could dramatically accelerate and intensify climate changes (Lewis 2006). For example Cox *et al.* (2000) argue that while rain forests are currently sinks for carbon, by the middle of the 21st century they may become carbon sources under global 'business as usual' emissions of CO_2.

While there has been an overall reduction in tropical forest area primarily due to deforestation over the last few decades, several studies have documented historical increases in tropical forest extent (Bowman *et al.* 2001, Eden & McGregor 1992, Endress & Chinea 2001, Furley 1992, Guillet *et al.* 2001, Russell-Smith *et al.* 2004). The obvious question is 'What are the drivers of the expansion of tropical forest boundaries?' Experimental attribution of the causes to changes to tropical forests is extremely difficult due to physical, financial and ethical constraints (Osmond *et al.* 2004). One approach shown to help narrow down hypotheses for the causes of forest dynamics is to examine the ecological 'fingerprint' of the changes. Different causes of change have different signatures that are evident in their field attributes (Banfai & Bowman 2005, Lewis *et al.* 2004). Investigating the field attributes of areas with different histories of vegetation change can therefore help to interpret the dynamics.

Kakadu National Park provides a model system to apply this methodology at a spatial scale large enough to capture heterogeneity in factors such as landscape setting, fire regime and soil type. A recent study of 50 rain-forest patches by Banfai & Bowman (2006) found that the rain-forest patches increased in size from 1964 to 2004 by an average of 28.8% (Figure 1a). Expansion was observed in both wet and dry rain-forest types, thus spanning the

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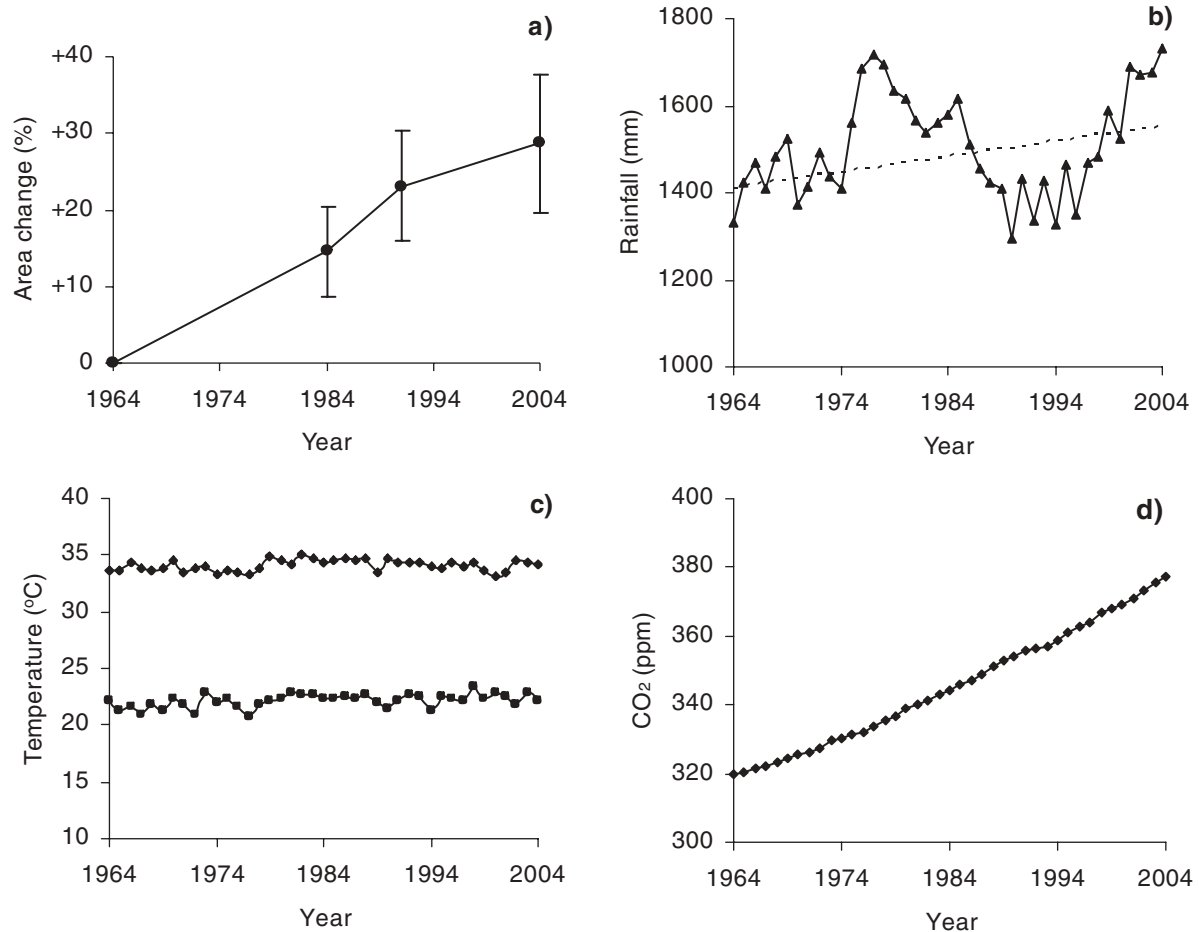[1] Corresponding author. Email: daniel.banfai@cdu.edu.au

Figure 1. Changes in area of rain forest in Kakadu National Park compared to trends of various climate variables. Percentage change (±SE) in rain-forest area over study period relative to 1964 (Banfai & Bowman 2006) (a). Five-year running average rainfall for Oenpelli, the closest rainfall station to Kakadu National Park with a complete record (Bureau of Meteorology 2003). The least squares regression line is also shown (b). Annual mean maximum and minimum temperatures recorded at Oenpelli (Bureau of Meteorology 2003) (c). Atmospheric CO_2 concentrations collected at Mauna Loa Observatory, Hawaii (Brook & Bowman in press) (d).

hydrological range of this vegetation formation. This general response was suggestive of a geographically widespread driver such as climate (i.e. increased rainfall and/or CO_2, Figure 1) or disturbance history (e.g. fire regime or feral animals) (Banfai & Bowman 2006). However, substantial uncertainty remained as to the relative importance of these various potential causes of change. It is extremely difficult to substantiate that global change is driving vegetation dynamics, and thus before embarking on such a quest it is prudent to ensure that more localised factors are not responsible for the observed change.

The purpose of this paper is therefore to investigate these competing hypotheses by determining the nature of the observed changes in terms of floristics, structure, environmental and disturbance correlates as measured in the field. Specifically we assess the hypotheses that rain-forest expansion: (1) occurs across a range of the geomorphic settings as measured by soil type and slope angle; (2) is not restricted to any particular species or

assemblage of species; (3) is not strongly related to specific levels of recent fire disturbance or feral animal impacts.

We argue that if all of the above hypotheses are consistent with the field attributes then this invites more serious consideration of global change phenomena and we suggest possible landscape modelling approaches to advance this problem. The results are also discussed in relation to the long-term stability of the rain-forest boundaries and the regional management of monsoon rain forests.

STUDY SITE

Kakadu National Park covers nearly 20 000 km^2 and is located on the north coast of the Northern Territory of Australia, 250 km east of Darwin (Figure 2). Two thirds of Kakadu National Park is comprised of lowland plains that flank the East, South and West Alligator Rivers. The vegetation of the Kakadu National Park area has
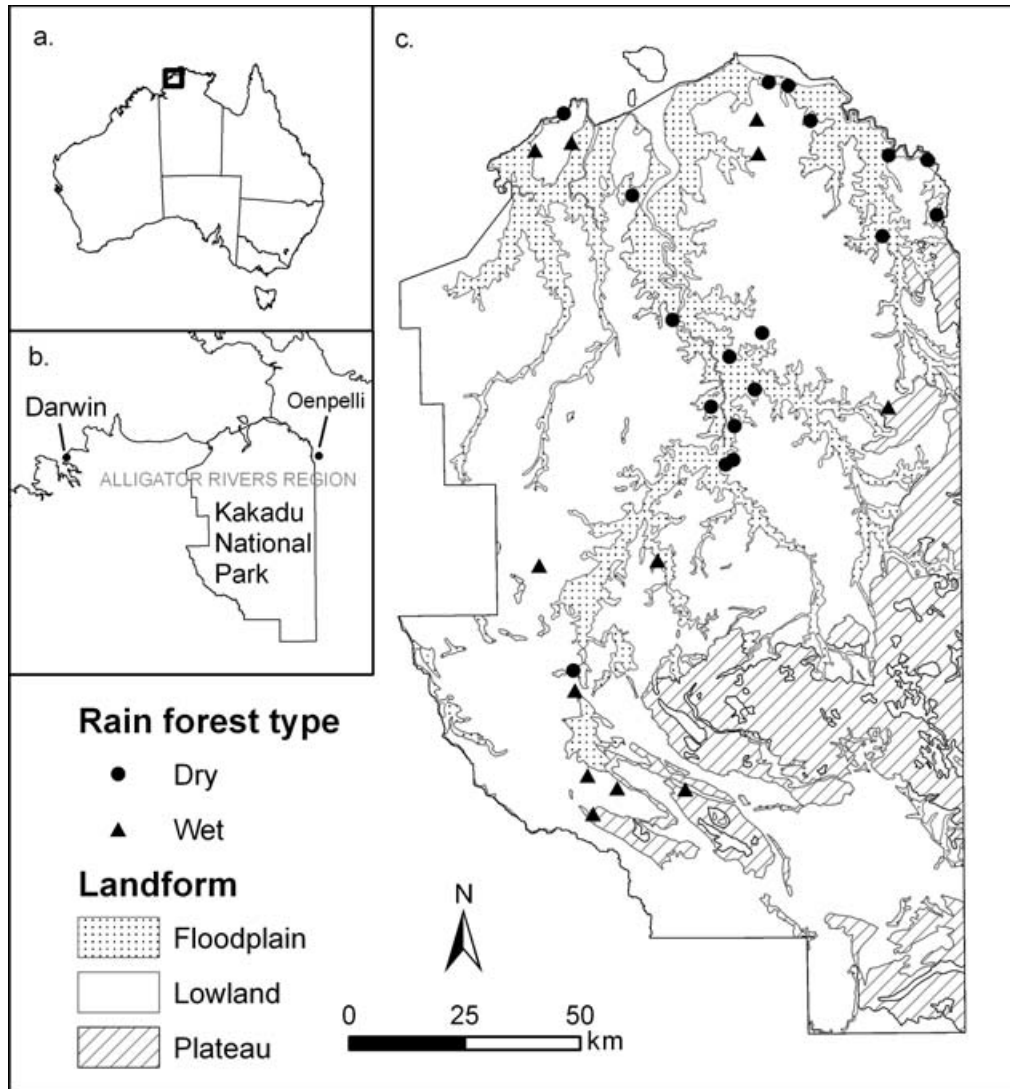
Figure 2. Location of study site in the Northern Territory of Australia (a), location of Kakadu National Park at the regional scale (b) and location of rain-forest patches sampled overlayed on the different landforms present in the study site (c).

been described by a large number of studies, including descriptions based on 'land systems' (Story 1976) and more recent studies based on mapping of faunal habitats (Schodde *et al.* 1987). On the lower reaches of the rivers occur large treeless seasonally flooded freshwater flood plains that grade into mangrove swamps and salt flats at the mouth of the rivers. The most abundant vegetation type is *Eucalyptus* savanna which occurs on the deeply weathered plains that flank the floodplains and abut the rugged western edge of the Arnhem Land Plateau. *Melaleuca* forests occur on seasonally inundated floodplain margins and form gallery forests along rivers and creeks, often grading into monsoon rain forest. The monsoon rain forest consists of hundreds of mostly small (<5 ha) patches scattered throughout the savanna matrix (Schodde *et al.* 1987).

In Australia the term 'rain forest' is used to define a broad variety of atypical Australian forest types including monsoon rain forests (Bowman 2000). The rain forests of the region have been described and classified in detail by Russell-Smith (1991). The two basic types of rain forest that occur in the Kakadu National Park lowlands are wet monsoon rain forest, which occurs on sites with perennial moisture supplies, and dry monsoon rain forest, which occurs on freely drained sites that are often associated with topographic fire protection such as rocky areas, cliff lines and hill tops (Bowman *et al.* 1991, Russell-Smith 1991). For simplicity we here refer to these vegetation types as 'wet rain forest' and 'dry rain forest'.

The region has a monsoonal climate with over 90% of the *c.* 1.5 m annual rainfall occurring in the wet season (October–March). Maximum daily air temperatures

remain high throughout the year (*c.* 35 °C) with cooler nocturnal temperatures occurring during the dry season (*c.* 20 °C) (Bureau of Meteorology 2003, Figure 1c).

The Kakadu National Park region has been continuously occupied by Aboriginal people for at least 50 000 y (Roberts *et al.* 1993). Fire was used to protect rainforest boundaries, however, traditional practices such as this have largely ceased following a major reduction in the Aboriginal population of the area when Europeans arrived around the middle of the 19th century (Press & Lawrence 1995). Aboriginal people currently live in small communities in the lowland savannas of Kakadu National Park, which is now jointly managed by the Traditional Owners and the Commonwealth government.

Fire records since settlement for the region are very sparse (Bowman *et al.* in press). Detailed information on fire frequency at the landscape scale is only available from 1980 onwards and is based on mapping of fire scars from satellite imagery. While the spatial resolution of those data was too coarse to be used in this analysis, it indicates that fire frequencies have been high throughout Kakadu National Park over the last two decades. For example, between 1980 and 1994, 55% of the lowland savanna habitats were burnt annually (Russell-Smith *et al.* 1997).

METHODS

Aerial photography

Rain-forest boundaries were mapped by Banfai & Bowman (2006) for each of the years 1964, 1984, 1991 and 2004 using a 20 × 20-m lattice grid. All photographs used colour film at a scale of 1:25 000 apart from 1964 which were black and white and at 1:16 000. The imagery was scanned from contact prints to achieve a common pixel resolution of 1 m². Each lattice grid point was manually classified into vegetation types for each year using ArcGIS 8 (ESRI) at a common scale of 1:3000, primarily based on the distance between tree crowns. Stereo view was not used.

Here field survey plots were centred on these grid points to compare the attributes of areas with different histories of vegetation change. For the purposes of this study we operationally define 'stable' plots as those that did not change vegetation type in any of the four photographic time-slices from 1964 to 2004. 'Transitional' plots were defined as those that changed between 1964 and 2004 from savanna to rain forest or vice versa. Analysis of the various combinations and permutations of change that occurred between these two endpoints would require an enormous sample size in order to be statistically robust and was therefore beyond the scope of this study. In any case consideration of the individual change trajectories would only be warranted if the current analysis indicated

that site-specific factors were important in understanding the landscape variation in the floristic composition of the boundaries.

Field sampling

Thirty rain-forest patches were selected for field sampling from the 50 rain-forest patches that were the subject of aerial photographic analysis. Full details of the sampling design of the 50 patches are provided in Banfai & Bowman (2006). Effort was made to ensure that field surveys were conducted across the full geographic range of lowland rain forest in the study site and that variation in fire regime and soil type was captured. Surveys were conducted in the dry season between May and October 2004.

Field survey plots were 20 × 20 m and centred on grid points used in the vegetation mapping, which were located in the field with a Global Positioning System (GPS). Individual rain-forest patches were stratified into four equal parts (north-south and east-west divisions) in order to spread the samples over the patch. Where possible, four random points (one from each quarter) of each vegetation type based on the 2004 aerial photography were sampled. Extra sample points were added to sample transitional sites based on the aerial photography record (maximum of 10 per site). A total of 588 points was sampled. Traditional owners were employed to assist with the surveys where possible.

Table 1 summarizes the variables recorded within each 20 × 20-m survey plot and the field measures used. Soil texture categories were adapted from McDonald *et al.* (1990). Flammable weed species recorded were *Sorghum* spp., *Pennisetum polystachion* (L.) Schult., *Urochloa mutica* (Forssk.) T. Q. Nguyen and *Andropogon gayanus* Kunth.

Table 1. Field measures for all variables recorded.

Variable	Field measure
Tree basal area	Sweep with Bitterlich wedge from centre of plot
Dominant species	Identity of each tree recorded with the Bitterlich wedge
Buffalo (*Bubalus bubalis*) impact; Pig (*Sus scrofa*) impact	Proportion of plot covered as either <1%, 1–5%, 6–25%, 26–50%, 51–75%, 76–99% or 100%
Cover >2 m; grass cover; flammable weed cover	Projective foliage cover measured on the same ordinal scale used for buffalo impact. Cover >2 m was recorded within a 5 × 5 m quadrat in the centre of each plot
Time since fire	0 = fire since last wet season, 1 = fire less than 5 y ago, 2 = fire more than 5 y ago, 3 = no evidence of fire
Soil texture	Surface (10 cm) as 1 = sand, 2 = sandy loam, 3 = loam, 4 = clay loam, 5 = clay

Voucher specimens of all species were collected and their identity confirmed at the Northern Territory Herbarium.

Framework for data analysis

It has been previously demonstrated that there was a clear floristic separation between dry and wet rain forests in the study site (Bowman *et al.* 1991, Russell-Smith 1991). All analyses were therefore performed separately for these two rain-forest types. As the vast majority of vegetation changes occurred between savanna and rain forest (Banfai & Bowman 2006), only transitions between these two vegetation types were considered. Where possible, analyses were based on patch averages; survey plots of the same vegetation change trajectory within a rain-forest patch were averaged to avoid bias toward patches with more samples. This also controls for the spatial autocorrelation of multiple samples within rain-forest patches. The following statistical tests were undertaken to address the various hypotheses regarding the expansion of rain forest.

Structural and floristic attributes

The average basal areas of rain-forest and non-rain-forest tree species were calculated for each vegetation transition based on a previous classification of species groups with a Two-way Indicator Species Analysis (TWINSPAN) procedure (Banfai & Bowman 2006). Benefits and limitations of this approach are discussed by Banfai & Bowman (2005). The average abundance of rain-forest trees, non-rain-forest trees and grass cover was calculated for each of the four possible vegetation changes between rain forest and savanna, and were compared with Kruskal–Wallis tests. Plots that were burnt since the last wet season were excluded from analyses of grass cover.

Blocked MRPP (MRBP) is a variant of the Multi-Response Permutation Procedure (MRPP) (Mielke 1991) that is able to account for floristic variation between rain-forest patches. MRBP was used to test the hypothesis that there was no difference in overall tree species composition between stable and transitional plots and whether there was an effect of proximity to the rain-forest and savanna boundary. Edges were defined as being within two grid points (*c.* 40 m) of the mapped rain-forest boundary. Edge and core plots were identified using Arcview 3.3 (ESRI). MRBP requires a balanced design with only one sample unit for each combination of block and treatment. To accommodate this, where several samples were taken of a particular transition at a rain-forest patch, one sample was randomly selected. This procedure was repeated five times and the median P value was calculated.

To investigate whether expanding rain-forest areas were dominated by particular species the proportion of the total basal area of the species in plots that changed from savanna to rain forest between 1964 and 2004 was ranked and averaged. Average basal area and average frequency was also calculated for the most abundant species. These rankings were repeated for stable rain-forest plots.

Effect of environmental and disturbance variables

The proportion of plots in each soil texture and time-since-fire category was calculated for each vegetation transition. Kruskal–Wallis non-parametric tests were used to assess differences in environmental and disturbance variables between different vegetation change trajectories. Plots that were burnt since the last wet season were excluded from analyses of flammable weeds.

Generalized linear models (GLMs) were used to further investigate the hypothesis that environmental and disturbance variables were not strongly related to vegetation transitions. GLMs are a generalization of linear regression models and have the advantage of allowing for a variety of distributions for the response and error terms in the model (McCullagh & Nelder 1989). Mixed-effect GLMs were used so that rain-forest patch could be coded as a random effect to account for the variance between patches. Predictor variables included in the models were chosen a priori in accordance with the Information Theoretic paradigm (Burnham & Anderson 2001). The fixed effects included were time since fire (factor), feral animal impact and soil type (factor). These particular variables were chosen as previous research had suggested that they may be good predictors of historical changes to rain-forest boundaries in the context of Kakadu National Park (Banfai & Bowman 2006). Interactions were not included in the models as we were primarily interested in the main effects at this stage in the investigation. The inclusion of interaction terms would also have made the number of parameters fitted by the models excessively large, inflating the amount of deviance explained by the models.

Different models were developed for savanna-to-rain-forest and rain-forest-to-savanna transitions, as the ecological processes involved in these transitions are fundamentally different (Brook & Bowman in press). (1) Savanna change model. The dependent variable of a binomial mixed-effects GLM (logit-link) was whether a savanna point changed to rain forest between 1964 to 2004 (coded as a 1), or remained savanna throughout (coded as a 0). (2) Rain-forest change model. This had the same structure as the savanna change model, except that the dependent variable was whether a rain-forest point changed to savanna between 1964 to 2004 (coded as a 1), or remained rain forest throughout (coded as a 0). The amount of deviance explained by the global models was then calculated for both rain-forest types.
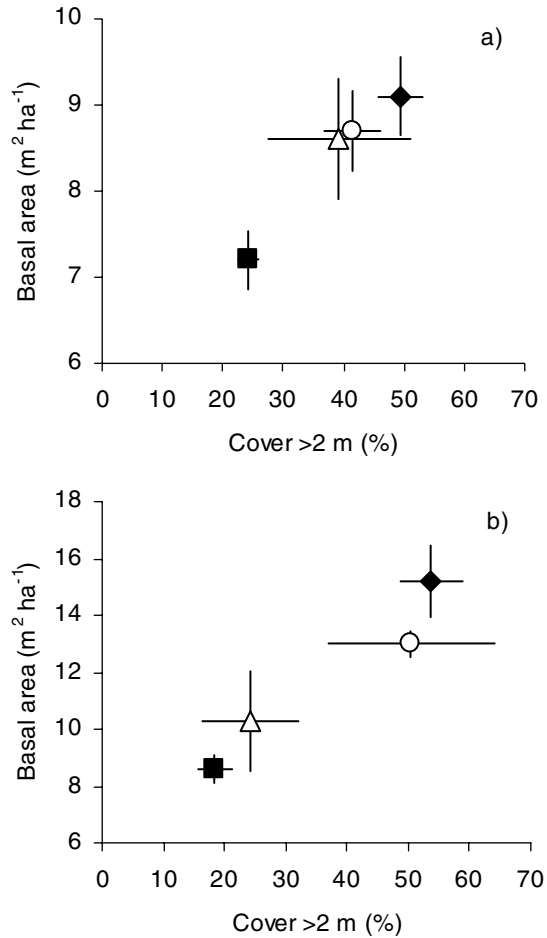
Figure 3. Percentage cover > 2 m is shown against basal area (with SE) for different trajectories of vegetation change between 1964 and 2004. (a) Dry rain forests; (b) Wet rain forests. Diamonds = Stable rain forest (RF); Squares = Stable Savanna (Sav); Circles = Sav to RF; Triangles = RF to Sav (N patches averaged for Dry rain forest RF-Sav = 7, Sav-RF = 15, Stable RF = 18, Stable Sav = 19; Wet rain forest RF-Sav = 7, Sav-RF = 6, Stable RF = 10, Stable Sav = 10).

RESULTS

Structural and floristic attributes

Stable wet rain forests had a much higher average basal area than stable dry rain forests (15.2 vs. 9.1 m^2 ha^{-1}) but were similar in terms of canopy cover (Figure 3). Basal area and cover were consistent with the mapped changes because the transitional plots had average values intermediate between the stable states for both rain-forest types. Similarly, the average abundance of rain-forest and non-rain-forest trees was also intermediate for the transitional plots (Figure 4). For example, in wet rain forests the density of rain-forest trees in stable savanna was 5.3 m^2 ha^{-1}, stable rain forest had 13.3 m^2 ha^{-1} while savannas that had changed to rain forest had an intermediate value of 10.9 m^2 ha^{-1}. Savannas that

became rain forests had a higher abundance of rain-forest trees relative to stable savannas for both wet and dry rain-forest types based on Kruskal–Wallis tests (dry rain forest H = 33.5, P < 0.001; wet rain forest H = 4.44, P = 0.035), while there was no significant difference in non-rain-forest trees. At least 10% of the basal area was non-rain-forest trees in sites classified as stable rain forest, and stable savanna plots notably had >50% rain-forest trees (Figure 4).

Grass cover showed the opposite trend to tree abundance for both rain-forest types (Table 2). For example, stable savannas surrounding dry rain forests had 22.1% grass cover which was significantly greater than savannas that had changed to dry rain forest which had 9% grass cover (H = 7.46, P = 0.007). For the transition from rain forest to savanna, the opposite differences were observed, with average grass cover being greater in transitional plots relative to stable rain forests, although these differences were not statistically significant (Table 2).

Rain-forest plots showed a consistent overall floristic difference to savanna plots at the P < 0.05 level for dry rain forest, but not for wet rain forest (Table 3). There were no significant floristic differences between edge and core samples for rain forest or savanna for both rain-forest types (Table 3). There were also no significant differences in the floristic composition between transitional plots and their stable counterparts.

Most of the dominant species in plots that changed from savanna to rain forest are classified as rain-forest species (Table 4). A few species were identified as having a particularly high average basal area and frequency in plots that changed from savanna to rain forest, however they only comprised a small proportion of the total basal area. For dry rain forest, these species included *Strychnos lucida* and *Erythrophleum chlorostachys* (Table 4). For wet rain forest, dominant species included *Lophostemon lactifluus*, *Xanthostemon eucalyptoides* and *Pandanus spiralis* (Table 4). The assemblage of dominant species was consistent with the ordination analysis that indicated transitional rain-forest areas had a similar floristic composition to stable areas.

Effect of environmental variables

Average slope was very low for all vegetation transitions (Table 2), with 90% of survey plots having a slope below 5°. No significant differences were observed between vegetation change trajectories for either rain-forest type. Both stable and transitional plots occur across a range of soil types (Figure 5). The majority (>68%) of dry rain-forest plots were on sandy loam soils, with a small proportion (<15%) on sand or clay. In contrast, wet rain forests had more variable soil types. For both
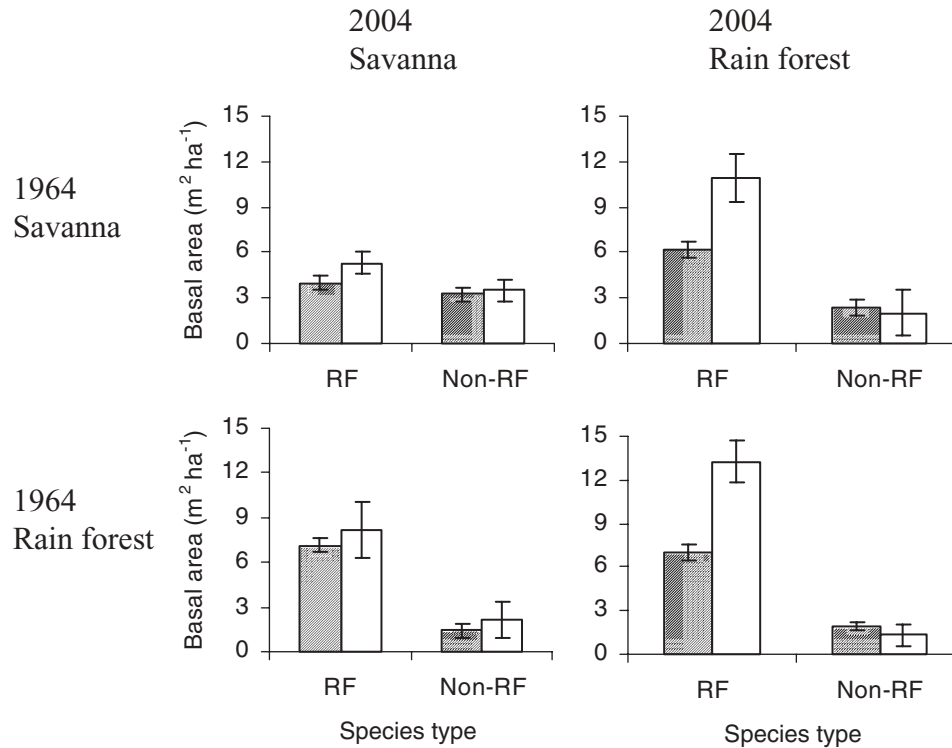
Figure 4. Abundance of rain-forest and non-rain-forest trees in dry rain forest (hatched bars) and wet rain forest (white bars) for different trajectories involving savanna and rain forest. The number of patches averaged for each transition is as in Figure 3.

rain-forest types, the different vegetation change trajectories were generally similar in their proportions of plots with different soil types. However, notably over 80% of wet rain forests that changed from savanna to rain forest were on sandy loam soils, with the rest being in clay soils (Figure 5).

Effect of disturbance variables

Evidence of fire was recorded in >70% of plots for all four vegetation change trajectories (Figure 6). It was particularly notable that most stable rain-forest plots had evidence of past fire. For all transitions, the majority of

Table 2. Mean ($\pm$ SE) for field attributes comparing different trajectories of vegetation change. Dry and wet rain-forest types are shown separately. Sav = savanna; RF = rain forest.

	Vegetation change			
Variable	Stable Sav	Sav to RF	Stable RF	RF to Sav
Dry rain forest				
Grass cover (%)	22.1 ± 4.92	9.0 ± 3.69	10.8 ± 2.61	29.5 ± 8.97
Flammable weed cover (%)	2.0 ± 1.96	0.1 ± 0.08	0.1 ± 0.07	2.8 ± 1.55
Pig impact (%)	38.3 ± 3.12	15.6 ± 5.29	16.7 ± 4.36	11.9 ± 16.6
Buffalo impact (%)	0.1 ± 1.34	0.2 ± 0.23	2.1 ± 1.96	1.5 ± 0.11
Total feral animal impact (%)	38.5 ± 3.31	15.8 ± 5.26	18.8 ± 4.57	12.9 ± 16.5
Slope (°)	0.8 ± 0.44	0.9 ± 0.24	2.1 ± 0.87	1.6 ± 0.41
N (plots)	161	68	103	11
Wet rain forest				
Grass cover (%)	56.2 ± 6.85	15.9 ± 12.5	26.2 ± 6.10	32.4 ± 18.8
Flammable weed cover (%)	0.3 ± 6.18	0.4 ± 0.38	1.3 ± 0.67	11.3 ± 0.33
Pig impact (%)	12.1 ± 2.17	13.4 ± 6.90	17.9 ± 8.50	5.3 ± 8.75
Buffalo impact (%)	0 ± 0.84	0 ± 0.00	0.4 ± 0.27	1.5 ± 0.00
Total feral animal impact (%)	12.1 ± 2.89	13.4 ± 6.90	18.3 ± 8.43	6.8 ± 8.75
Slope (°)	2.7 ± 0.56	2.1 ± 0.82	4.1 ± 1.03	2.2 ± 0.83
N (plots)	47	11	58	10

Table 3. Blocked MRPP results comparing floristic composition of rain forest and savanna, edge and core samples, as well as comparing transitional samples to their stable counterparts. The two rain-forest types are shown separately.

Comparison	N (patches)	Median P
Dry rain forest		
Rain forest vs. savanna	19	0.003
Rain forest (edge vs. core)	18	0.899
Savanna (edge vs. core)	18	0.137
Stable RF vs. Sav–RF	7	0.787
Stable Sav vs. RF–Sav	14	0.126
Wet rain forest		
Rain forest vs. savanna	10	0.170
Rain forest (edge vs. core)	7	0.158
Savanna (edge vs. core)	10	0.332
Stable RF vs. Sav–RF	7	0.230
Stable Sav vs. RF–Sav	6	0.072

plots were evidently burnt less than 5 y ago. There also was no systematic relationship between time since fire and vegetation change transition, with only minor differences in the proportions of the different categories of time since fire between the different vegetation transitions for both wet and dry rain forest. This indicates that the probability of recent fire was not substantially different for the four vegetation transitions (Figure 6).

The cover of flammable weeds was very low (<3%) for almost all vegetation change transitions in both rain-forest types (Table 2). Only wet rain-forest plots that changed from rain forest to savanna had a slightly higher average weed cover (11.3%).

The vast majority of feral animal impact was from pig rooting (Table 2). Buffalo impact was generally negligible with an average of less than 2.5% buffalo impact cover

Table 4. Rain-forest species ranked by average proportion of total basal area (BA) comparing plots that changed from savanna to rain-forest between 1964 and 2004 to those that remained rain forest for both rain-forest types. Asterisks (*) indicate classified as rain-forest species. N patches averaged for savanna to rain forest = 15; stable rain forest = 18.

| Species	Prop. BA (%)	BA (m^2 ha^{-1})	Freq. (%)
Savanna to dry rain forest			
Strychnos lucida R. Br.*	8	0.7	42
Erythrophleum chlorostachys (F. Muell.) Baill.	7	0.9	24
Corymbia polysciada (F. Muell.) K. D. Hill & L. A. S. Johnson*	6	0.4	24
Syzygium suborbiculare (Benth.) T. G. Hartley & L. M. Perry*	6	0.5	22
Corymbia bella K. D. Hill & L. A. S. Johnson	5	0.5	17
Barringtonia acutangula (L.) Gaertn.*	5	0.2	14
Alstonia actinophylla (A. Cunn.) K. Schum.*	5	0.3	31
Acacia auriculiformis A. Cunn.*	4	0.3	15
Stable dry rain forest			
Strychnos lucida R. Br.*	9	0.9	41
Erythrophleum chlorostachys	8	0.4	23
*Syzygium suborbiculare**	5	0.3	11
*Acacia auriculiformis**	4	0.4	15
Canarium australianum F. Muell.*	4	0.3	23
*Alstonia actinophylla**	4	0.4	25
Terminalia microcarpa Decne.*	3	0.4	17
Vitex acuminata R. Br.	3	0.2	13
Savanna to wet rain forest			
Lophostemon lactifluus (F. Muell.) Peter Wilson & J. T. Waterh.*	26	3.0	50
Xanthostemon eucalyptoides F. Muell.*	11	0.7	33
Pandanus spiralis R. Br.*	9	1.5	56
Melaleuca leucadendra (L.) L.*	6	2.1	8
Eucalyptus tetrodonta F. Muell.	5	1.1	25
Erythrophleum chlorostachys	5	0.9	17
Eucalyptus miniata A. Cunn. ex Schauer	4	0.8	17
Lophostemon grandiflorus (Benth.) Peter Wilson & J. T. Waterh.*	4	0.4	8
Stable wet rain forest			
*Xanthostemon eucalyptoides**	17	2.1	49
*Melaleuca leucadendra**	10	2.7	41
Syzygium nervosum DC.*	10	2.0	37
*Pandanus spiralis**	6	1.1	28
*Lophostemon lactifluus**	6	1.3	28
Erythrophleum chlorostachys	6	0.8	25
Gmelina schlecteri H. J. Lam*	5	1.1	28
Eucalyptus alba Reinw. ex Blume*	3	0.4	14
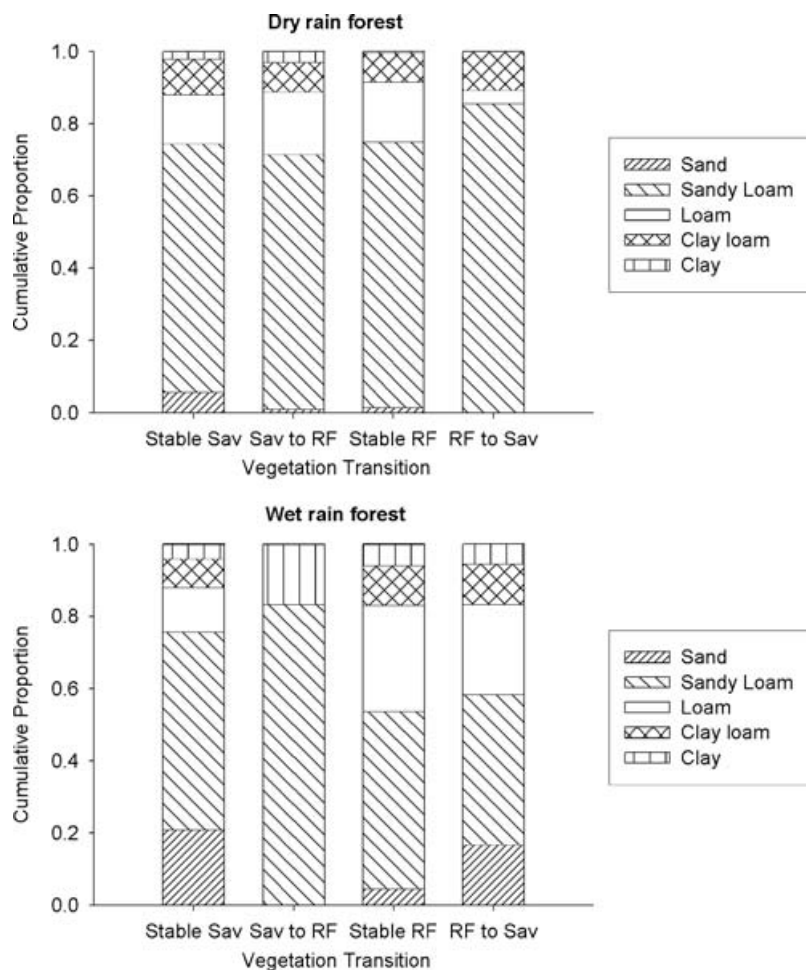
Figure 5. Proportion of plots with different soil texture for each vegetation transition. Dry and wet rain-forest types are shown separately. RF = rain forest; Sav = Savanna (Total N plots averaged for dry rain forest RF–Sav = 11, Sav–RF = 68, Stable R = 103, Stable S = 161; wet rain forest RF–Sav = 10, Sav–RF = 11, Stable R = 58, Stable S = 47).

for all vegetation change trajectories. For dry rain forests, feral animal impact was highest for stable savannas (38.5%), while for wet rain forests it was highest for stable rain-forest areas (18.3%). Average feral animal damage was lowest for the transition from rain forest to savanna for both rain-forest types (Table 2).

Kruskal-Wallis tests showed no significant difference between vegetation change trajectories for any of the disturbance variables at $P < 0.05$ for either rain-forest type. Additionally, the deviance explained by the models including both disturbance and environmental variables was very low for both dry and wet rain forest. In the case of dry rain forests, the savanna change model explained 6.8% of the deviance, while the rain-forest change model explained 4.3%. For wet rain forest, the savanna change model explained 2.3% of the deviance, while the rain-forest change model explained 11.4%.

DISCUSSION

Structural and floristic attributes

Areas that changed from savanna to rain forest between 1964 and 2004 were associated with an increase in rain-forest trees and a decrease in grasses, relative to stable savannas. This can be interpreted as suppression of grasses by woody species, which acts to reduce fire frequency and intensity (Stott 2000). The opposite relationship between rain-forest tree abundances and grass cover was observed for the transition of rain forest to savanna when compared with stable rain forests. The reduction in grass cover in areas where rain-forest expansion has occurred is expected given the general inability of grass to establish beneath a closed canopy, and is consistent with the inference of Hennenberg *et al.*
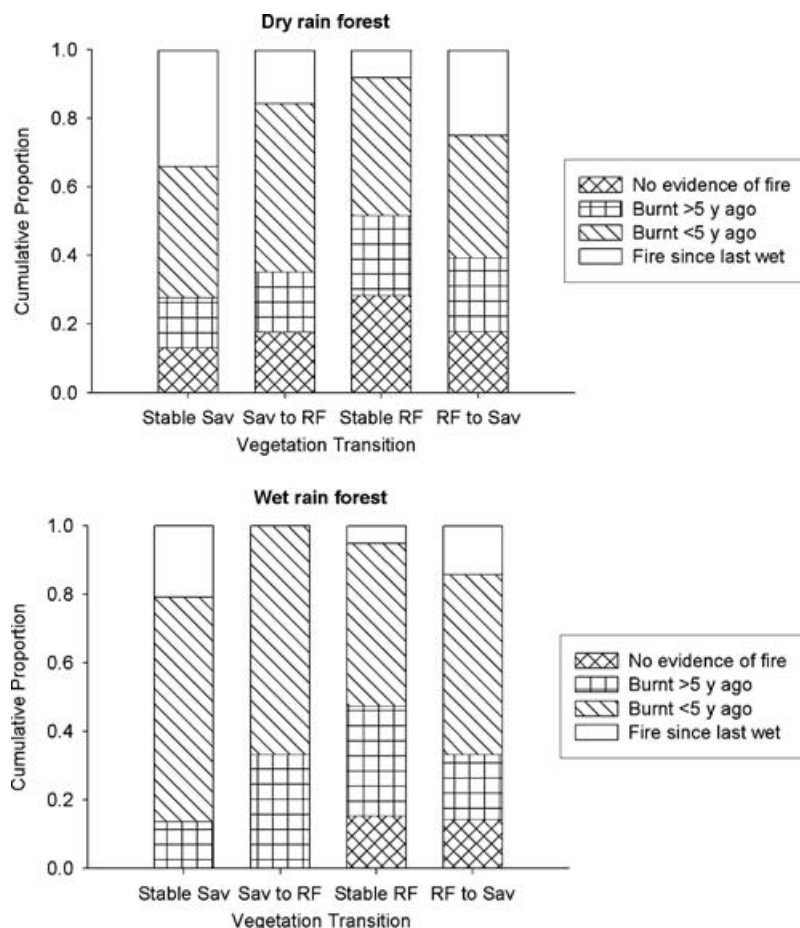
Figure 6. Proportion of plots with different time since fire for each vegetation transition. Dry and wet rain-forest types are shown separately. RF = rain forest; Sav = savanna (N plots averaged is as in Figure 5).

(2006) who analysed transects across forest-savanna boundaries in the Comoe National Park, Ivory Coast. In this study we have been able to verify these relationships as we have knowledge of the recent boundary dynamics based on historical aerial photography.

Rain forests that established since 1964 were found to be very similar in their assemblage of species to longer established rain forest given (1) there was little overall difference in floristics between transitional plots and their stable counterparts and (2) areas where rain-forest expansion had occurred were dominated by a similar assemblage of species to stable rain-forest areas. Further, there was a substantial proportion of both rain-forest and non-rain-forest trees in plots classified as 'stable'. For stable savanna this is most probably the result of historical fluctuations in the position of the rain-forest boundary where large rain-forest trees have become stranded in the savanna following rain-forest boundary retreat. Likewise, the non-rain-forest trees in the 'stable' rain forest may either be relics of forest expansion that occurred prior to 1964, or are the result of savanna incursion into the

rain forest between 1964 and 2004 which has allowed non-rain-forest species to become established.

In aggregate these observations support the view that rain-forest boundaries in Kakadu National Park are highly dynamic, with colonization of areas surrounding rain forests by a range of rain-forest species occurring rapidly at the decadal scale. This is consistent with previous studies documenting that a large proportion of the rain-forest species in northern Australia are highly vagile, with the ability to rapidly colonize new areas. For example, diverse rain-forest assemblages occur frequently on recently evolved landforms such as stabilized beach dunes and riverine floodplains (Bowman & Panton 1993, Russell-Smith & Lee 1992).

Effect of environmental variables

The field attributes suggested that the expansion of rain forests over the last 40 y has been little influenced by environmental factors. The rain-forest expansion

occurred across a range of soil types and there was little systematic difference in soil texture between vegetation change trajectories. There was however a tendency for savanna to change into wet rain forest on sandy loam soils. Such a relationship is to be expected as this rain-forest type is likely to have established in the wettest, most suitable areas before spreading to more marginal, freely draining soils. These results are consistent with transect studies in three dispersed regions ranging from Central America, the northern Amazon Basin and the central Brazilian plateau, where soil nutrient status was related to, but did not necessarily determine, the position of the forest–savanna boundary (Furley 1992).

Slope was also similar between vegetation change trajectories at the rain-forest boundary. The low slope values recorded were expected given the lowlands of Kakadu National Park consist of predominantly flat sedimentary plains (Williams 1969). This contrasts to other landscape settings with more topographic relief where slope and aspect are thought to be important determinates of rain-forest habitat suitability (Brook & Bowman in press, Puyravaud *et al.* 1994). In sum, the similarity of environmental attributes between different vegetation transitions reinforces the view that Kakadu National Park provides a model system for investigating the relative importance of other factors driving landscape change.

Effect of disturbance variables

Disturbance factors measured in the field showed no ecologically consistent relationships with the rain-forest boundary dynamics. For example, there was little systematic difference in the evidence of recent fire between the four vegetation change trajectories. This is inconsistent with studies where the local dynamics of the forest–savanna boundary zone were inferred to be primarily a function of fire incidence (Furley 1992, King *et al.* 1997, Ratter 1992). Such a result may reflect the ability of many rain-forest species to survive at least a single fire (Bowman 1991, Russell-Smith *et al.* 2004). Thus fire frequency (which was not determined) rather than simply time since fire is probably of more importance in influencing the probability of vegetation change (Bowman 2000).

Flammable weeds were recorded as their high biomass can greatly increase the frequency and intensity of fires (Stott 2000). However, the cover of flammable weeds was consistently very low across the different vegetation transitions, suggesting that they are not a major factor influencing the rain-forest boundaries. Nonetheless it is notable that both patches that contracted in area greater than 5% between 1964 and 2004 both had flammable weeds present. The one patch that experienced

the greatest overall contraction (−18%) was the only site to have *Urochloa mutica* recorded, and also infestations of *Pennisetum polystachion*, which are both highly flammable introduced weeds. The other patch that contracted substantially had no introduced flammable weeds but had a large proportion of its boundary surrounded by the native annual grass *Sorghum* spp., which is also thought to be related to high fire frequency and intensity (Russell-Smith *et al.* 2003, Yibarbuk *et al.* 2001). These results signal that management of flammable weeds around rain-forest boundaries should remain a priority for land managers.

There was also relatively little recent feral animal impact recorded in all vegetation change transitions, with the vast majority of the damage being from pig rooting. The fact that average feral animal impact was lowest in plots that had contracted from rain forest to savanna for both rain-forest types is not consistent with the hypothesis that the contraction of rain forest is associated with high feral animal impact. The general lack of buffalo impact contrasts with regional surveys conducted in the 1980s by Russell-Smith & Bowman (1992) where severe damage attributable to buffalo and cattle impact was recorded at 20.4% of sites. The reduction in buffalo impact is probably related to the major drop in buffalo numbers from culling during the Brucellosis and Tuberculosis Eradication Campaign in the 1980s (Skeat *et al.* 1996).

The modelling confirmed that contemporary disturbance and environmental factors measured in the field are poor predictors of historical vegetation transitions on rain-forest boundaries. However, this study has only focused on the biological endpoint of disturbance histories at the local (plot) scale. It must be admitted that a limitation of this analysis is insufficiently detailed historical information on fire impacts and feral animal distributions. Nonetheless, there is the opportunity to use a GIS approach to further examine variation in rain-forest dynamics at the patch scale. For example, an index of buffalo impact on rain-forest patches could be derived from buffalo tracks observed on historical aerial photography. Proxies for fire activity could also be used such as fire scar mapping from satellite imagery which dates back to 1980 (Russell-Smith *et al.* 1997).

Conclusions

The similarity of newly established rain forest to more stable rain forest in Kakadu National Park and the lack of environmental limits to change suggest that the current trend of rain-forest expansion will continue if current climatic trends and disturbance regimes persist. This is supported by previous detailed floristic and biogeographical studies of monsoon rain forests in northern Australia indicating that these forests currently

only occupy a fraction of their potential domain (Bowman 2000).

It remains unclear as to whether the rapid expansion of rain-forest boundaries in Kakadu National Park represents a short-term fluctuation of boundaries that are stable on a longer time scale, as has apparently occurred on Croker Island near the boundary of the Park (Bowman *et al.* 2004). Stable isotopes in soil at Croker Island led Bowman *et al.* (2004) to argue that rain-forest boundaries had been 'stable' at the millennial scale, yet tiny fragments of rain forest and abandoned 'nests' of *Megapodius reinwardt* were interpreted as evidence of short-term fluctuations in the location of the boundary. They hypothesized that the episodic expansion and contraction of rain forest was related to fluctuations in cyclonic disturbance and rainfall cycles where wetter periods allow rain-forest species to grow at sufficient rates to colonize the savanna despite recurrent fire disturbance. The rain-forest dynamics in Kakadu National Park may also be responding to similar long-term climate-driven cycles.

The limited effect of environmental and disturbance variables on the probability of rain-forest boundary expansion in Kakadu National Park is consistent with the ubiquitous effect of global change. Factors such as increased atmospheric CO_2 (Figure 1d) may have contributed to the observed changes as it is known to preferentially advantage trees (mostly C_3 photosynthetic pathway) over grasses (mostly C_4), shifting the balance toward trees on the savanna–forest boundary (Berry & Roderick 2002). For example, seedlings of *Maranthes corymbosa* Blume, a rain-forest species that occurs in Kakadu National Park, showed a marked increase in growth in a doubled CO_2 environment with total shoot dry weight increasing by 163% (Berryman *et al.* 1993). The expansion of rain-forest tree species into savanna may have been favoured given the evidence that they have higher rates of assimilation and faster growth rates than eucalypts (Prior *et al.* 2003, 2004). The rain-forest expansion is also correlated with an increase in annual rainfall over the last few decades (Banfai & Bowman 2006, Figure 1b). Increased rainfall may have contributed to the rain-forest expansion as increased soil moisture can promote rain-forest species establishment in the surrounding savanna and is an important determinant of the location of forest–savanna boundaries in tropical regions (Bowman & Panton 1993, Furley 1992).

Substantial uncertainty remains as to the relative importance of the various potential drivers of rain-forest boundary dynamics in Kakadu National Park. For example, although time since fire was a poor predictor of historical vegetation transitions in this study, there is a need to investigate the effect of fire frequency. Historical feral animal impacts may also have had a major effect on the rate of rain-forest boundary change that could not

be detected in contemporary field surveys. Additionally, the relationship between the rate of boundary dynamics and fluctuations in rainfall has not yet been explored. An appropriate methodology to tease out the relative importance of these factors will be spatially explicit modelling that incorporates information from a number of different thematic layers (Augustin *et al.* 2001, Brook & Bowman in press).

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