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Rainforest expansion reduces understorey plant diversity and density in open forest of eastern Australia

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Abstract The expansion of rainforest pioneer trees into long-unburnt open forests has become increasingly widespread across high rainfall regions of Australia. Increasing tree cover can limit resource availability for understorey plant communities and reduce understorey diversity. However, it remains unclear if sclerophyll and rainforest trees differ in their competitive exclusion of understory plant communities, which contain most of the floristic diversity of open forests. Here, we examine dry open forest across contrasting fire histories (burnt and unburnt) and levels of rainforest invasion (sclerophyll or rainforest midstorey) to hindcast changes in understorey plant density, richness and composition. The influence of these treatments and other site variables (midstorey structure, midstorey composition and soil parameters) on understorey plant communities were all examined. This study is the first to demonstrate significantly greater losses of understorey species richness, particularly of dry open-forest specialists, under an invading rainforest midstorey compared to a typical sclerophyll midstorey. Rainforest pioneers displaced over half of the understorey plant species, and reduced ground cover and density of dry forest specialists by ~90%. Significant understorey declines also occurred with increased sclerophyll midstorey cover following fire exclusion, although losses were typically less than half that of rainforest-invaded sites over the same period. Understorey declines were closely related to leaf area index and basal area of rainforest and wattle trees, suggesting competitive exclusion through shading and potentially belowground competition for water. Around 20% of displaced species lacked any capacity for population recovery, while transient seed banks or distance-limited dispersal may hinder recovery for a further 68%. We conclude that rainforest invasion leads to significant declines in understorey plant diversity and cover in open forests. To avoid elimination of local native plant populations in open forests, fires should occur with sufficient frequency to prevent overstorey cover from reaching a level where shade-intolerant species fail to thrive.

Key words: competition, fire frequency, succession, time since fire, understorey plant communities, woody encroachment.

INTRODUCTION

The expansion of rainforest pioneer trees into the open forests and woodlands of northern, eastern and southern Australia has been observed for many decades (Gilbert 1959; Smith & Guyer 1983; Fensham & Fairfax 1996; Rose & Fairweather 1997; Russell-Smith *et al.* 2004b; Banfai & Bowman 2005) – a phenomenon referred to as rainforest invasion (e.g. Bowman 2000; Russell-Smith *et al.* 2004b) or encroachment (e.g. Rosan *et al.* 2019). Causes of rainforest invasion are typically associated with reductions in disturbances (fire and herbivory) that otherwise limit rainforest tree density (Sankaran *et al.* 2005; Hoffmann *et al.* 2009; Dantas *et al.* 2016), or with increased resources that benefit rainforest tree establishment, including atmospheric CO_2 and rainfall (Bond & Midgley 2000; Bowman *et al.* 2010; Wigley *et al.* 2010). Recent models articulate the interactions between disturbance and resources in regulating rainforest cover (Murphy & Bowman 2012; Hoffmann *et al.* 2012a), greatly advancing understanding of vegetation patterns in fire-prone landscapes (Archibald *et al.* 2018). Understanding the consequences of rainforest expansion into open forests is critically important due to the high biodiversity values of open forests (Kier *et al.* 2005; Murphy *et al.* 2016) and carbon storage capacity (Santín *et al.* 2015; Moroni *et al.* 2017). Open-forest biomes are in sharp decline globally (Hoekstra *et al.* 2005), and rainforest expansion contributes to this decline through state transitions to closed rainforests that are difficult to reverse (Scheffer *et al.* 2001; Butler *et al.* 2014).

Open forests, woodlands and savannas (hereafter *open forests*) are characterised by an 'open' tree

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canopy, above a shade-intolerant understorey plant community comprising assemblages of graminoids, forbs and shrubs (Specht & Specht 1999; Bond & Parr 2010; Veldman *et al.* 2015). These understorey plant communities contain the majority of ecosystem plant diversity, provide key forage, shelter and nesting habitat for fauna, and the fine fuel needed for fires of sufficient frequency to maintain ecosystem structure and diversity (Veldman *et al.* 2015; Murphy *et al.* 2016). In these systems, regular disturbance (fire and herbivory) promotes high understorey density and richness, by preventing competitive exclusion of grasses, forbs and shrubs by taller woody plants (Woinarski *et al.* 2004; Ratajczak *et al.* 2012). Without disturbance, however, tree cover progressively increases, reducing light, water and nutrient availability for understorey plant species (Specht & Morgan 1981; Hart *et al.* 2005; Jackson *et al.* 2007; Close *et al.* 2009). Accordingly, the likelihood of canopy closure increases in regions where fire frequency has been reduced by cessation of aboriginal burning, fragmentation and fire suppression (e.g. Fire Ecology Working Group 2002; Butler *et al.* 2014; Baker & Catterall 2015).

Canopy closure and understorey declines in open forest can result from increased densities of either sclerophyll trees typical of open forest (e.g. Specht & Specht 1989; Lunt 1998a; Shackelford *et al.* 2015) or from fire-sensitive rainforest pioneers expanding from nearby rainforest areas (e.g. Woinarski *et al.* 2004; Parr *et al.* 2012). While the intensity of competition is most often attributed to tree density, rainforest trees are reported to have a higher capacity than open-forest trees to suppress understorey plants in African and North American savannas (Veldman *et al.* 2013; Hiers *et al.* 2014; Charles-Dominique *et al.* 2018). Rainforest trees differ from open-forest trees with regard to crown architecture (e.g. crown area, Rossatto *et al.* 2009; branch mass per area, Charles-Dominique *et al.* 2018), light capture (e.g. specific leaf area, Prior *et al.* 2003; Hoffmann *et al.* 2005) and water use (Bowman *et al.* 1999). Yet, it remains unclear if these functional groups differ in their effects on understory plant communities in Australian open forests.

The long-term consequences of rainforest invasion on understorey plant communities depend not only on the extent of species displacement, but also the capacity of displaced species to re-establish standing plant populations. Species and ecosystem recovery are dependent on the seed pool available for recolonisation, which in turn is controlled by seed-bank persistence and capacity for dispersal from remote populations (Auld *et al.* 2000; Kirkman *et al.* 2004). Species lacking persistent soil seed banks become locally extinct with the death of adult plant populations (Noble & Slatyer 1980; Keith 1996), while recovery of species with soil seed banks is dependent on the lifespan of the seed bank exceeding the time to the next fire (Keith 1996; Auld *et al.* 2000). For species unable to maintain in-situ populations, recovery is dependent on seed dispersal from remote populations, which may be severely limited for species with distance-restricted dispersal, such as gravity- and ant-dispersal mechanisms (Kirkman *et al.* 2004), especially in landscapes fragmented by land-use change. Such traits are common in fire-prone ecosystems, where plant traits that improve the persistence of individuals through frequent fire have evolved at the expense of long-distance dispersal and colonisation (Bond & Midgley 2001; Zaloumis & Bond 2011).

Although many studies document rainforest expansion globally and in Australia (e.g. Smith & Guyer 1983; Puyravaud *et al.* 2003; Parr *et al.* 2012; Stanton *et al.* 2014; Butler *et al.* 2014; Rosan *et al.* 2019), very few Australian studies provide quantitative data on its effects on understorey plant communities in the open forest. Furthermore, we know of no such study in Australia which examines whether open-forest trees and rainforest pioneers differ in their effects on open-forest understory plant communities. The aims of this study were to quantify the impacts of rainforest expansion on plant diversity in dry open forest in Bundjalung National Park, subtropical coastal eastern Australia, and to compare these impacts with those due to canopy closure by non-rainforest trees.

In this study, we quantify changes in understorey species richness and composition following divergent trajectories of canopy closure in dry open forest. We ask the following questions:

1. Is increased midstorey tree cover generally associated with altered community composition and reduced plant cover, density and species richness of understorey plant communities?
2. Is increased rainforest pioneer cover in the midstorey associated with reduced understorey plant cover, density and species richness?
3. Does canopy closure reduce the richness and abundance of species with limited seed storage and/or dispersal capacity and hence, the capacity for recovery of understorey communities with the return of fire?

METHODS

Study area and landscape context

The study was conducted in Bundjalung National Park on the north coast of New South Wales, Australia (153.33°E, 29.25°S). The study area lies within the Bundjalung Wilderness Area (NSW *Wilderness Act* 1987), which

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comprises an extensive mosaic (~38 000 ha) of old-growth coastal forest and heathland. Soils comprise grey, brown and yellow podzolic soils forming gently undulating rises of low elevation (5–20 m) and gentle slopes (2–3%; Morand 2001). The vegetation of the study area is tall dry sclerophyll forest (eastern dry shrubby subgroup, Keith & Pellow 2015) dominated by *Eucalyptus signata*, with *Corymbia intermedia*, *Eucalyptus siderophloia*, *Angophora woodsiana* and *Lophostemon suaveolens* also common. Heathy vegetation has dominated the landscape since the early Holocene (8700 ± 60 years BP, McGrath & Boyd 1998). Prior to 1994, the study area was characterised by sparse-canopied open forest with a dense heathy ground layer, as verified by three lines of evidence, including full floristic survey plots (Griffith 1983), fine-scale vegetation mapping (Griffith & Wilson 2011) and historical aerial photography (1953, 1958 & 1966). Since 2001, however, a north–south fire management track has contained recent wildfires to the eastern half of the study area. To the east, regularly burnt forests have retained a dense heathy ground layer below a sparse midstorey, while in fire-excluded forests to the west, a dense midstorey of young trees occurs above a sparse ground layer. Additionally, post-fire midstorey succession in unburnt forests has followed two different trajectories, with a midstorey dominated by either: (i) bird-dispersed rainforest pioneers, occurring where forests are connected by unbroken forest cover to proximate (<1 km) rainforest tree populations along the Esk River, or (ii) sclerophyll trees, where forests are separated by non-forested vegetation from distant (>1.5 km) rainforest tree populations (A. G. Baker, pers. comm., 2018). This contrasting fire history and forest structure provides a useful case study for examining the relationship between time since fire, midstorey composition and understorey plant communities.

Site selection

We selected 24 sites, located across three fire and midstorey classes: (i) burnt forest with open midstorey (*burnt open*, $n = 12$), (ii) unburnt with a dense midstorey dominated by sclerophyll trees (*unburnt-sclerophyll*, $n = 6$) and (iii) unburnt with a dense midstorey dominated by rainforest pioneers (*unburnt-rainforest*, $n = 6$; Fig. 1). Unburnt sites were last burnt in 2001 (16 years before our study), with burnt forest having three fires over the same period (16, 10 and 4 years before this study). Sampling was constrained to areas with a historical canopy cover between 30% and 70% (i.e. open forest, Walker & Hopkins 1990) as visually estimated on historical aerial photographs (1958 and 1966). Sampling was also restricted to the *E. signata* forest type of Griffith and Wilson (2011) to reduce environmental variability and constrained to locations mapped as *Candidate Old Growth* (NPWS 2001) to minimise influence from historical land use. Within this area, site locations were randomly selected using the Create Random Points feature in ArcMap version 10.5 (Environmental Systems Research Institute, 2014, Redlands, CA, USA), and constrained by fire history and midstorey composition, while preserving maximum distance between sites (178 ± 37 m) to minimise autocorrelative effects.

Tree cover sampling

All field data were collected between November 2017 and March 2018. At each of the 24 site locations, we used a nested plot design fixed along a 50 m centre line. Transects were oriented to maximise distance between neighbouring sites. To quantify canopy and midstorey structure, the diameter at breast height (DBH, 1.3 m above ground) of each tree, shrub or vine ≥2 m tall was recorded in three DBH size classes (i.e. <10, 10 ≤ 30 and >30 cm) in 2, 20 and 40 m wide quadrats, respectively. Recorded stems were identified to species to characterise composition and tallied to quantify stem density (stems ha^{-1}). Stem DBH and density were used to calculate basal area (m^2 ha^{-1}) across the four stem diameter classes. All measures of midstorey basal area were derived from stems <10 cm DBH. Tree crown height, crown base height, crown width and crown separation were measured for midstorey (2–12 m; $n = 30$ trees per site) and canopy (>12 m; $n = 10$) strata (Catana 1963; Walker & Hopkins 1990). From these, means were derived for midstorey crown cover, total crown cover and midstorey crown height. For analysis, all plots were standardised to per hectare unit area.

To examine how functional composition of the midstorey influences understorey plant communities, trees were classified into functional groups based on descriptions in Harden (1990): open forest (e.g. *Eucalyptus*, *Allocasuarina*, *Lophostemon*), rainforest (e.g. *Glochidion ferdinandi* and *Alphitonia excelsa*) and wattles (*Acacia disparrima* and *A. leiocalyx*; Appendix S1). Wattles was placed into a separate intermediate group, because the two *Acacia* species present have contrasting habitat associations (*A. disparrima* – rainforest margins, wet sclerophyll forest and sclerophyll woodlands; *A. leiocalyx* – sclerophyll forest and heath (Harden 1990), but typically co-occurred in high abundance in both unburnt treatments. The rainforest species are pioneers and are most common around rainforest edges.

Canopy closure at each site was measured using hemispherical photographs taken at five points, 10 m apart, along the centre line of the plot during even cloud cover to maximise delineation between canopy vegetation and sky (Jonckheere *et al.* 2005). Photographs were taken with a camera (Canon 5D Mark II, Lensbaby 5.8 mm f/3.5 Circular Fisheye Lens) positioned level at a height of 1 m and orientated to north. At this height, the canopy of tree saplings and adults is recorded, but not the ground layer. The images were analysed using Gap Light Analyzer v 2 (Cary Institute of Ecosystem Studies, Millbrook, NY, USA) for leaf area index (LAI, Frazer *et al.* 1999). Values were averaged over the five samples to give a single value for each 0.2 ha plot.

Understorey community sampling

Understorey vegetation (ground layer and lower midstorey, ≤5 m tall) was characterised in a 2 × 50 m plot to provide measures of both species richness and plant density. All recorded individuals were identified to species in the field or collected for subsequent identification. Plant nomenclature follows Harden (1990). Plant density was derived by recording distance along quadrat where each new species

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Fig. 1. Different fire and midstorey classes in Bundjalung National Park: (a) burnt forest with open midstorey (four years post-fire), (b) unburnt with dense sclerophyll midstorey (16 years post-fire) and (c) unburnt with dense rainforest midstorey (16 years post-fire).

was first encountered, converted to density m^{-1} and summed for all species encountered within the plot. Saplings of overstorey trees (mature height >5 m; Harden 1990) were excluded from the understorey data set, to limit analyses to understorey taxa.

Functional response to an increase in overstorey cover was assessed by classifying understorey plants according to their habitat association using (Harden 1990): dry open-forest specialists (occurring only in dry sclerophyll forests or more open habitats), open-forest generalists (occurring in both dry and wet sclerophyll forests, but rarely or never occurring in rainforest) and rainforest associates (occurring in rainforest, but may also occur in open forest; Appendix S2). Understorey plants were also classified into one of three growth forms: graminoid, forb or shrub.

Ground cover was sampled within 1 m^2 subplots, using the same camera location and position to characterise LAI, but using a Canon 17–40 mm f/4 L wide-angle lens (Tokyo, Japan), angled vertically downward. Images were analysed using Canopeo v 2.0 (Oklahoma State University, Stillwater, USA) to determine fractional green canopy cover (FGCC; Patrignani & Ochsner 2015).

Soil sampling

To allow for underlying soil influences that may be independent of fire and midstorey classes, five soil cores evenly spaced along the transect were collected at each site using a handheld soil auger. From these cores, samples were taken at depths of 10 and 50 cm, bulked by depth, and then subsampled for each site. Particle size distributions were determined using laser diffraction (Mastersizer 2000; Malvern Instruments Ltd, Malvern, UK; Arriaga *et al.* 2006), and calibrated by defining clay as <2 μm, silt as 2–20 μm and sand as >50 μm. Soil pH, phosphorus and conductivity were analysed using the methods of Rayment and Lyons (2011).

Analysis

Differences in vegetation structure, species composition and soil parameters between midstorey classes were tested using Kruskal–Wallis rank sum tests and Conover–Iman post hoc tests with Bonferroni correction. Statistical analyses were processed using R software (v.3.4.2.; R Foundation for Statistical Computing, Vienna, Austria) and the package PMCMR (Pohlert 2018).

Univariate (species richness) and multivariate (community) analyses were undertaken using PRIMER-E (v. 6.1.13) and the PERMANOVA+ (v. 1.0.3) add on (Clarke & Gorley 2006; Anderson *et al.* 2008). Our sampling design comprised two factors: fire (between blocks, two levels, fixed) and midstorey (block) nested within fire (two levels in unburnt, one level in burnt, fixed). Environmental variables were $\log(x + 1)$-transformed and normalised to account for unit variation. Variables with high multicollinearity (>0.9) were identified and removed via inspection of draftsman plot correlation tables (Clarke & Gorley 2006), before calculating a Euclidean distance resemblance matrix. Biological response variables were square-root transformed to reduce excessive influence of particularly common taxa (Clarke 1993). Resemblance matrices for biological data were calculated using either Euclidean distance (univariate data) or zero-adjusted Bray–Curtis similarity (multivariate, Clarke *et al.* 2006).

We tested for differences in understorey plant composition between fire and midstorey classes using permutational multivariate analysis of variance (PERMANOVA). To determine the relative influence of environmental factors on understorey composition, we used the distance-based linear model (DistLM) routine in PRIMER-E. Model selection used the step-wise procedure and AICc selection criterion (Anderson *et al.* 2008). To identify significant structural groups among sites, cluster analysis with similarity profile (SIMPROF) permutation tests was used. Three environmental variables with a consistently high proportion of variance scores in DistLM marginal tests were selected to determine their Pearson correlation coefficients with univariate measures of species richness and density using 'R' version v.3.4.2. All means are reported as mean ± SE (SEM).

To examine ability of locally extinct plant populations to re-establish standing plant populations at a site, understorey plants were assigned to recovery capacity classes according to seedbank type and seed dispersal mechanisms (Appendix S2), including no identified capacity (plants with neither persistent seed bank or wide dispersal), dispersal only (plants without persistent seed banks but capable of wide dispersal), seed bank only (plants with persistent seed bank, but incapable of wide dispersal) and seed bank or dispersal (plants with both persistent seedbank and wide dispersal capacity). Presence–absence comparisons between

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midstorey classes were limited to understorey plants recorded on at least two burnt sites.

RESULTS

Tree cover and soils across midstorey types

We found significant differences between fire and midstorey classes for 10 of the 12 vegetation structure parameters examined (Table 1a): leaf area index, midstorey crown cover midstorey height and all measures of basal area. We found no differences between midstorey classes for canopy crown cover, total crown cover or any measured soil variables. Leaf area index (LAI), midstorey (DBH <10 cm) crown cover, midstorey height and midstorey basal area were significantly higher for unburnt midstorey classes (sclerophyll and rainforest) than burnt open midstorey, although it did not differ between sclerophyll and rainforest midstorey (Table 1; Fig. 2). Measures of tree cover that were significantly higher in rainforest than open midstorey forest includes leaf area index (156% higher, $P < 0.001$), midstorey crown cover (45% higher, $P < 0.001$) and basal area midstorey trees (~4 times higher, $P < 0.001$). Rainforest midstorey forest had higher basal area of rainforest pioneers, compared with open (~39 times higher, $P < 0.001$) and sclerophyll midstorey (~15 times higher, $P < 0.001$) (Fig. 2; Table 1a). Total crown cover, canopy crown cover and all soil parameters showed no significant differences between any midstorey type (Table 1a).

Understorey plant diversity across midstorey types

In all, 140 plant taxa were recorded across all 24 sites, of which 73% were understorey plants and

Table 1. Parameter values (mean ± SE) and tests of significance (Conover–Iman post hoc tests with Bonferroni correction) for (a) vegetation structure and (b) understorey species richness, density and cover: open = burnt with open midstorey; sclerophyll = unburnt with sclerophyll midstorey; and rainforest = unburnt with rainforest midstorey

Parameter	Open	Sclerophyll	Rainforest	Open *vs.* sclerophyll	Open *vs.* rainforest	Sclerophyll *vs.* rainforest
(a)						
Leaf area index	1.05 ± 0.12	2.31 ± 0.13	2.69 ± 0.18	<0.001	<0.001	n.s.
Midstorey crown cover (%)	69.78 ± 3.26	101.43 ± 2.75	101.16 ± 2.87	<0.001	<0.001	n.s.
Midstorey height (m)	3.9 ± 0.18	6.81 ± 0.48	5.57 ± 0.3	<0.001	<0.001	n.s.
Basal area (m^2 ha^{-1})						
Total	36.45 ± 4.76	37.78 ± 1.93	54.02 ± 4.57	n.s.	0.006	n.s.
<10 cm Ø	2.61 ± 0.53	11.09 ± 1.25	12.24 ± 0.8	<0.001	<0.001	n.s.
10–30 cm Ø	2.88 ± 0.34	9.19 ± 1.98	5.89 ± 0.55	<0.001	0.002	n.s.
>30 cm Ø	30.95 ± 4.69	17.5 ± 1.7	35.89 ± 5.14	0.015	n.s.	0.002
Rainforest <10 cm Ø	0.16 ± 0.09	0.4 ± 0.27	6.01 ± 0.98	n.s.	<0.001	<0.001
Wattle <10 cm Ø	0.55 ± 0.13	3.91 ± 0.96	4.96 ± 0.5	<0.001	<0.001	n.s.
Sclerophyll <10 cm Ø	1.9 ± 0.52	6.78 ± 1.44	1.26 ± 0.4	0.008	n.s.	0.007
Canopy crown cover (%)	98.37 ± 5.59	87.43 ± 7.89	77.54 ± 8.68	n.s.	n.s.	n.s.
Total crown cover (%)	168.14 ± 6.68	188.85 ± 8.63	178.7 ± 8.68	n.s.	n.s.	n.s.
Sand >20 μm ISSS (%)	69.69 ± 1.9	70.76 ± 0.81	70.69 ± 1.37	n.s.	n.s.	n.s.
Silt 2–20 μm ISSS (%)	18.53 ± 0.5	16.64 ± 1.31	15.28 ± 1.36	n.s.	n.s.	n.s.
Clay <2 μm (%)	9.27 ± 0.47	9.43 ± 0.98	8.7 ± 1.17	n.s.	n.s.	n.s.
Phosphorus (mg/kg P)	2.25 ± 0.4	2.1 ± 0.42	1.64 ± 0.28	n.s.	n.s.	n.s.
pH	5.4 ± 0.13	5.34 ± 0.08	5.17 ± 0.13	n.s.	n.s.	n.s.
Electrical Cond. (dS/m)	0.04 ± 0	0.03 ± 0	0.03 ± 0	n.s.	n.s.	n.s.
(b)						
Species richness/100 m^2						
Total	37.92 ± 1.72	26.67 ± 1.05	18.67 ± 1.73	<0.001	<0.001	0.031
Dry forest specialists	31.92 ± 2.03	22 ± 1.77	7.17 ± 1.05	0.007	<0.001	0.009
Open-forest generalists	4.25 ± 0.46	2.83 ± 0.75	3.5 ± 0.5	n.s.	n.s.	n.s.
Rainforest associates	1.75 ± 0.22	1.83 ± 0.6	8 ± 0.77	n.s.	<0.001	<0.001
Graminoid	16.33 ± 0.97	11.17 ± 0.54	6.67 ± 0.56	<0.001	<0.001	0.010
Shrub	12.08 ± 0.96	8.83 ± 0.98	4.5 ± 0.96	n.s.	<0.001	0.035
Forb	4.42 ± 0.4	2.17 ± 0.4	1.5 ± 0.34	<0.001	<0.001	n.s.
Recovery-limited species	29.67 ± 2	19.50 ± 1.06	9.17 ± 1.3	0.0042	<0.001	0.0094
Plant density (m^{-2})						
Total	40.94 ± 2.8	18.77 ± 1.99	7.48 ± 1.6	<0.001	<0.001	0.014
Dry forest specialists	36.6 ± 3.41	16.16 ± 1.75	3.27 ± 1.15	<0.001	<0.001	0.009
Ground cover (%)	30.52 ± 2.02	14.69 ± 2.67	3.05 ± 0.44	<0.001	<0.001	0.009

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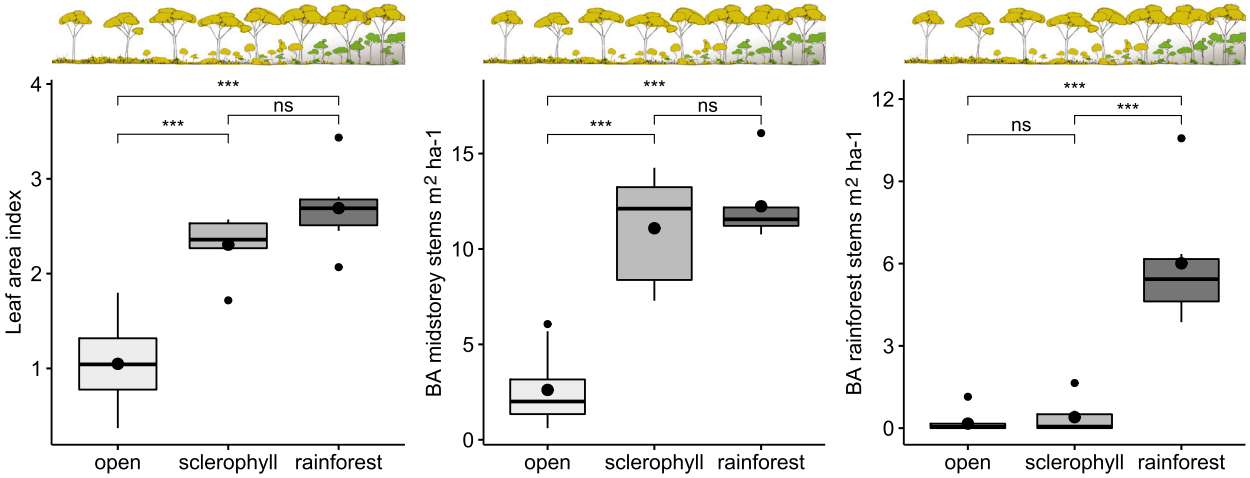

Fig. 2. Overstorey structure across three midstorey classes (burnt with open midstorey, unburnt with sclerophyll midstorey and unburnt with rainforest midstorey) showing leaf area index, basal area of midstorey stems and basal area of rainforest stems. Shown are median (horizontal line within box), mean (circle within box), 25th and 75th percentile (box boundaries), highest and lowest values (whiskers), outliers (circle outside box) and statistical significance ($^{\star}P < 0.05$, $^{\star\star}P < 0.01$, $^{\star\star\star}P < 0.001$, $^{ns}P > 0.05$).

27% overstorey trees and vines. Graminoids, shrubs and forbs comprised 37%, 33% and 13% of understorey plants, respectively (Appendix S1). Habitat associations of understorey plants comprised dry open-forest specialists (76%), open-forest generalists (8%) and rainforest associates (16%).

Total species richness differed significantly among midstorey classes ($F_{1,21} = 16.82$, $P < 0.001$; Appendix S3; Fig. 3), with the rainforest midstorey lower than open midstorey (51% lower, $P < 0.001$) and sclerophyll midstorey (30%, $P < 0.001$, Table 1b). Diversity of dry open-forest specialists was significantly affected by midstorey type ($F_{1,21} = 69.17$, $P < 0.001$; Appendix S3; Fig. 3), being lower under the rainforest midstorey than open midstorey (78%, $P < 0.001$) and sclerophyll midstorey (67%, $P < 0.001$, Table 1b). Diversity of rainforest associates was higher beneath rainforest midstorey than both open and sclerophyll midstorey ($P < 0.001$). Richness of open-forest generalists did not differ significantly between any midstorey classes. Among plant growth forms, species richness was lower under rainforest than open midstorey for graminoids (59%, $P < 0.001$), shrubs (63%, $P < 0.001$) and forbs (66%, $P < 0.001$, Fig. 3; Table 1b). Overall community composition differed significantly among midstorey classes ($F_{1,21} = 75.99$, $P < 0.001$, Appendix S3).

Similarly, all measures of understorey density and cover were significantly lower on unburnt than burnt sites, and significantly lower beneath rainforest than sclerophyll midstorey (Table 1b). Ground cover differed significantly among midstorey classes ($F_{1,21} = 5.68$, $P < 0.001$, Appendix S3), with rainforest midstorey lower than open midstorey (90% lower, $P < 0.001$) and sclerophyll midstorey (79%, $P < 0.001$). Plant density was lower under rainforest than open midstorey, including for total density (81.7% lower, $P < 0.001$) and dry forest specialist density (91.1%, $P < 0.001$).

Relationships between understorey plants and tree cover

Overall species richness and species richness of dry forest specialists, graminoids, shrubs and recovery-limited species were lower in forests with greater leaf area index, and basal area of rainforest pioneers and wattles (Fig. 4). Distance-based linear modelling (DistLM) found that variation in total species richness was best explained by basal area of wattles and rainforest pioneers in combination with total basal area (Table 2a; Appendix S4). Richness of dry forest specialists was best explained by rainforest basal area, leaf area index and total crown cover (Table 2a; Appendix S4).

For all analysed components of understorey composition (total, graminoid, shrub and forb), basal area of rainforest pioneers was included as the strongest predictor in all selected models (Table 2b; Appendix S4). For overall understorey composition, DistLM revealed that 39.7% of variation was explained by rainforest basal area (32.6 %) and leaf area index (7.1%) (Table 2b; Fig. 5). The distance-based redundancy analysis configuration (Fig. 5) shows moderate separation of unburnt from burnt sites with increasing leaf area index, while increasing

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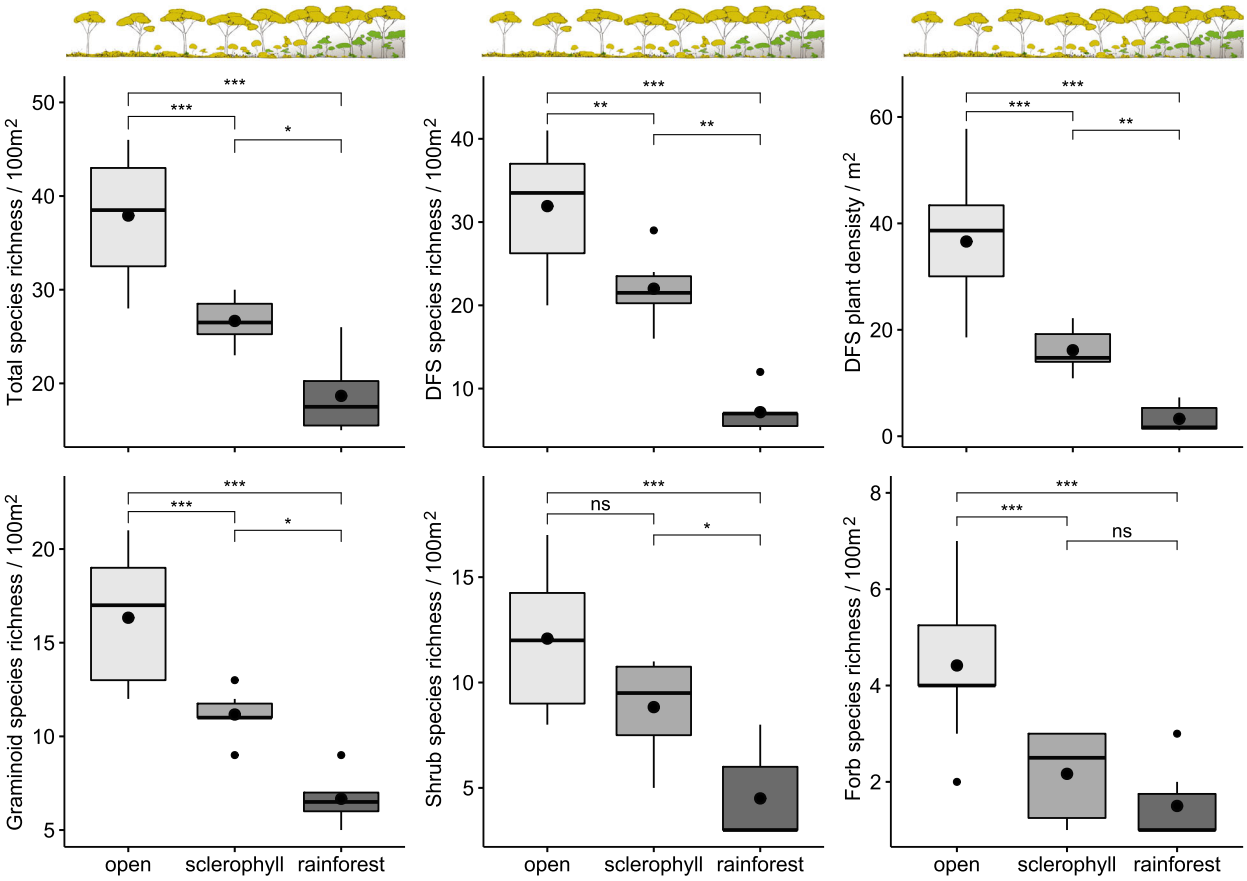

Fig. 3. Understorey species richness and plant density across three midstorey classes (burnt with open midstorey, unburnt with sclerophyll midstorey and unburnt with rainforest midstorey) shown for dry forest specialists (DFS), graminoids, shrubs and forbs. Shown are median (horizontal line within box), mean (circle within box), 25th and 75th percentile (box boundaries), highest and lowest values (whiskers), outliers (circle outside box), $*P < 0.05$, $**P < 0.01$, $***P < 0.001$; ns = no significant difference).

rainforest basal area strongly separates rainforest midstorey sites from both open and sclerophyll sites. SIMPROF cluster analysis clustered rainforest sites separately from both open and sclerophyll sites at a 30% similarity cut-off.

Potential for recovery of absent taxa

Diversity of recovery-limited species was significantly lower in unburnt midstorey classes than in the burnt class, and significantly lower in the rainforest than the sclerophyll class (Table 1b), being 69% lower under rainforest than open midstorey ($P < 0.001$). Among understorey taxa recorded in burnt forests (recorded at ≥2 sites), 30 (34%) were absent from sclerophyll midstorey sites and 52 (59%) were absent from rainforest midstorey sites (Fig. 6). Of species absent beneath rainforest midstorey, a total of 86% of species were identified as recovery-limited. Of these, ten species (19%) had no identified capacity to recover from the loss of adult plants (i.e. no persistent seed bank or wide dispersal) and included *Leptospermum polygalifolium*, *Banksia oblongifolia*, *Lomatia silaifolia*, *Burchardia umbellata*, *Xanthorrhoea fulva*, *Haemodorum austroqueenslandicum*, *Hakea actites*, *Stackhousia viminea*, *Thysanotus tuberous* and *Tricoryne elatior*. Recovery potential is limited for a further 35 (67%), including one species (*Lindsaea linearis*) dependent on wide dispersal, and 34 species dependent on soil seed banks in the absence of wide dispersal mechanisms. Differences in recovery-limited species richness were significant across midstorey types, being more than 50% lower beneath rainforest than sclerophyll midstorey ($P < 0.001$), and almost 35% lower beneath sclerophyll than open midstorey ($P = 0.004$, Table 1b).

DISCUSSION

Although numerous studies have documented the phenomenon of rainforest invasion into Australian open forests (e.g. Smith & Guyer 1983; Fensham &

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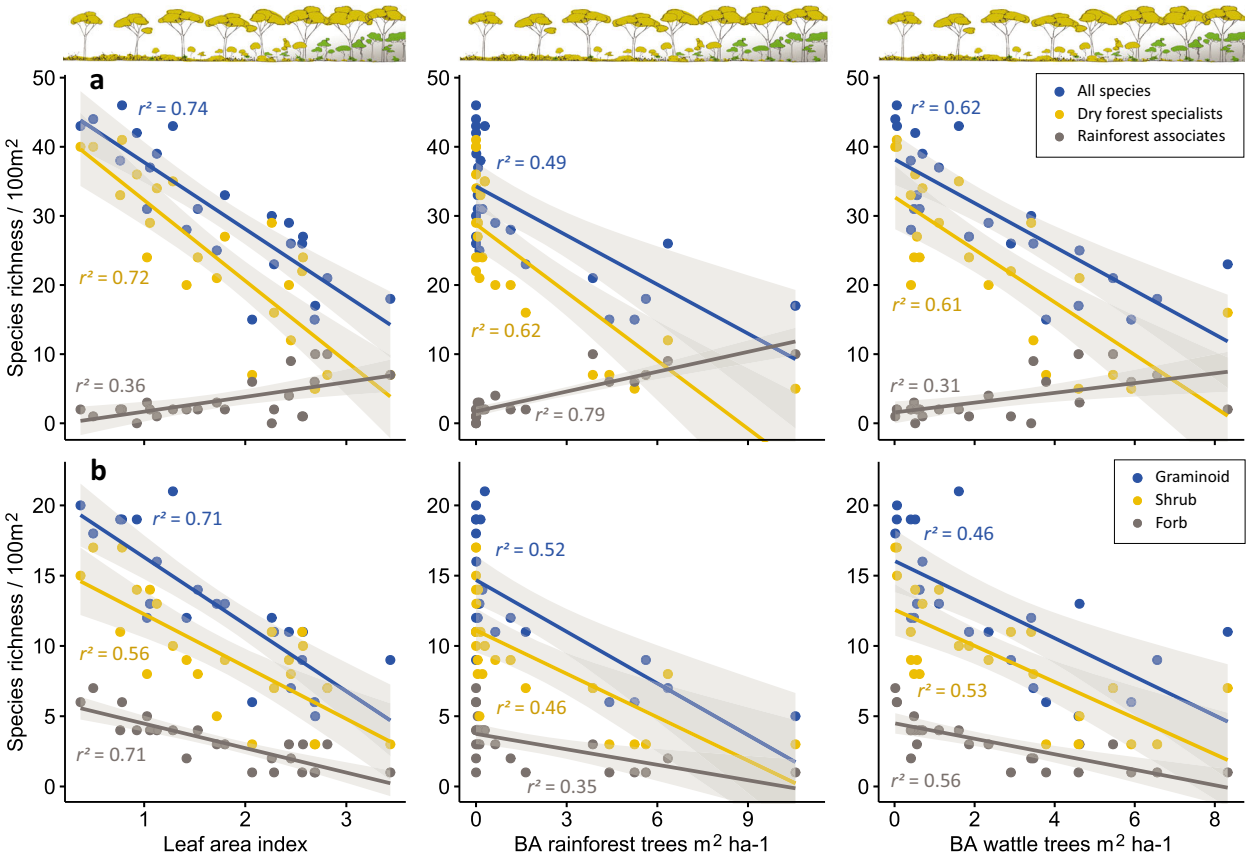

Fig. 4. Effect of leaf area index, rainforest tree basal area and wattle tree basal area on understorey species richness for (a) habitat association and (b) plant growth form. Estimated effect (blue, yellow or grey lines), 95% confidence intervals (grey shading) and Pearson correlation (r^2) are shown. All variables were significantly correlated ($P < 0.05$).

Fairfax 1996; Fensham & Butler 2004; Russell-Smith *et al.* 2004b), few have examined its effects on understorey plant communities (Rose & Fairweather 1997; Lewis *et al.* 2012), and none have compared these with canopy closure by sclerophyll trees. By including tree functional identity in our experiment, our findings extend this literature to show that a midstorey of rainforest trees exerts additional negative control over understorey plant communities in open forest. We found that an invading midstorey of rainforest pioneers in a dry open forest of eastern Australia has displaced around half of the understorey plant species, most of which have limited capacity for population recovery. Significant understorey declines also occurred beneath a closed midstorey of sclerophyll trees, although losses were generally half that of rainforest-invaded sites over the same period.

Our study design capitalised on the availability of replicate sites within a historically homogeneous open forest (Griffith 1983; Griffith & Wilson 2011) that has diverged into communities with distinct understorey vegetation in the last 20 years, coincident with changes in the fire management regimes. Acknowledging the limitations of space-for-time studies in demonstrating cause (Pickett 1989), rainforest invasion was nevertheless associated with a number of changes in the understory that are consistent with previous studies of woody encroachment on other continents. Understorey plant losses can occur with canopy closure by either open- or closed-forest (rainforest) trees (e.g. Ratajczak *et al.* 2012; Veldman *et al.* 2013). In Australia, the decline of understorey communities with increasing sclerophyll tree and shrub cover has been widely reported, including for species of *Allocasuarina* (Lunt 1998b; Shackelford *et al.* 2015; Bargmann and Kirkpatrick 2015), *Acacia* (wattles; Lunt 1998a; Costello *et al.* 2000) and *Leptospermum* (Price & Morgan 2008; O'Loughlin *et al.* 2015). Similarly, rainforest invasion has been widely reported to displace understorey plant communities in savannas globally (e.g. Parr *et al.* 2012; Veldman *et al.* 2013; Abreu *et al.* 2017) and northern Australian savannas (e.g. Woinarski *et al.* 2004; Russell-Smith *et al.* 2004a). We know of only two studies documenting similar declines in rainforest-invaded open forests of south-eastern Australia (Rose & Fairweather 1997; Lewis *et al.* 2012), although they did not compare the influence of functional midstorey

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Table 2. Distance-based linear models for understorey (a) species richness and (b) community composition: basal area (BA) and leaf area index (LAI), corrected Akaike Information Criterion (AICc), *F* value by permutation (Pseudo-F), *P*-values based on 999 permutations, estimates of components of variation (%, Prop. Var.), residual degrees of freedom (res.df)

Environ factor	AICc	Pseudo-F	*P*	Prop. Var.	res.df	R^2
(a)						
Overall species richness						
BA wattles	40.66	45.72	**0.001**	0.68	22	0.84
BA rainforest	31.60	13.17	**0.002**	0.13	21	
BA total	29.51	4.63	0.050	0.04	20	
Dry forest specialist richness						
BA rainforest	57.03	145.40	**0.001**	0.87	22	0.92
LAI	51.84	8.08	**0.012**	0.04	21	
Total crown cover	49.56	4.83	**0.027**	0.02	20	
(b)						
Understorey composition						
BA rainforest	174.34	10.62	**0.001**	0.33	22	0.40
LAI	174.29	2.49	**0.001**	0.07	21	
Graminoid composition						
BA rainforest	171.04	9.67	**0.001**	0.31	22	0.38
LAI	171.04	2.43	**0.001**	0.07	21	
Shrub composition						
BA rainforest	181.76	8.84	**0.001**	0.29	22	0.37
BA 10–30 cm	181.43	2.75	**0.002**	0.08	21	
Forb composition						
BA rainforest	179.75	8.07	**0.001**	0.27	22	0.27

Bold indicates that *P*-value is significant at 0.05.

composition. Together with these studies, our results suggest that understorey decline from rainforest invasion may be universal across both savanna and open-forest biomes of Australia.

Our results show that irrespective of overstorey composition, increased shade is likely to be an important determinant of understorey decline, with leaf area index the strongest individual predictor of understorey species richness, density and ground cover. Numerous studies show that reduced light intensity beneath tree cover reduces species richness by competitive exclusion of shade-intolerant understorey species (e.g. Gleadow & Ashton 1981; Specht & Morgan 1981; Barefoot *et al.* 2019). In open forest, regular disturbance (fire in this case) constrains overstorey tree cover by limiting growth of saplings into the overstorey, thereby limiting their ability to intercept light and competitively exclude grasses, forbs and shrubs via shading (Hoffmann *et al.* 2012a). Without fire, trees experience physiological and demographic release into the overstorey, severely limiting resource availability to the understorey. Other potential drivers of understorey decline associated with tree encroachment include increased transpiration and soil water use (Guarin & Taylor 2005; Bucci *et al.* 2008), heavy litter fall (Lunt 1998a; Price & Morgan 2008; Veldman *et al.* 2014) and altered nutrient availability (May & Attiwill 2003; Hart *et al.* 2005; Adams 2007).

Ours is the first study to show that invasion of rainforest pioneers into Australian open forest can cause significantly greater declines in understorey plant community diversity and density, than canopy closure by open-forest trees alone. Studies comparing the relative influence of open- and closed-forest (rainforest) trees in other continents have similarly found that rainforest trees exert greater competitive pressures on understorey vegetation (e.g. Veldman *et al.* 2013; Charles-Dominique *et al.* 2018). Relative to open-forest trees, rainforest trees can exert greater shading through various mechanisms, including faster radial crown growth and larger crown area for a given basal area (Rossatto *et al.* 2009), faster accumulation of leaf area (Hoffmann & Franco 2003), greater light interception per unit biomass (e.g. higher stem density, Charles-Dominique *et al.* 2018, higher specific leaf area, Prior *et al.* 2003; Hoffmann *et al.* 2005) and more continuous tree crown cover (Scholes & Archer 1997; Peterson & Reich 2008). While this aligns well with shading as a primary driver of understorey decline, distance-based linear modelling in our study consistently found basal area of rainforest pioneers explained declines better than LAI, suggesting mechanisms additional to shading.

In addition to aboveground competition, other studies indicate that rainforest trees may also be competitively superior belowground, including through increased surface root competition (Harvest

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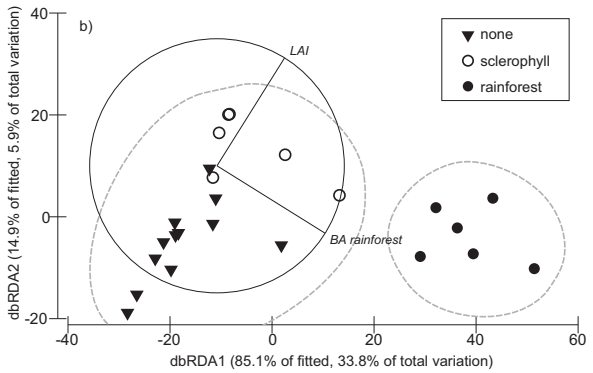

Fig. 5. Distance-based redundancy analysis (dbRDA) plot showing the environmental variables (basal area rainforest trees and basal area sclerophyll trees) fitted to the variation in understorey composition in burnt with open midstorey (triangles), unburnt with sclerophyll midstorey (open circles) and unburnt with rainforest midstorey (closed circles) in dry open forest in Bundjalung National Park. Vectors indicate the direction and strength (line length) of effect. SIMPROF cluster analysis overlay (30% similarity, dashed ellipses) defines significant separation of rainforest midstorey sites from all remaining sites.

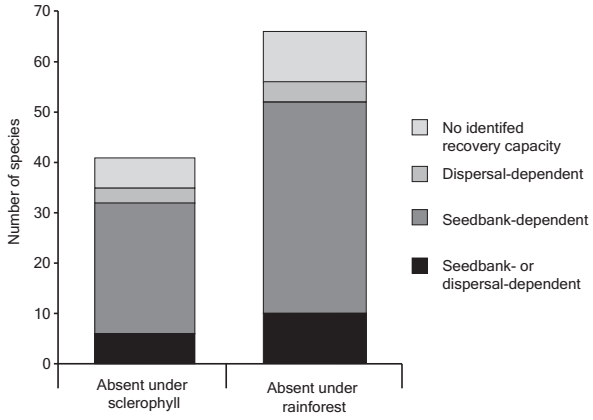

Fig. 6. Number of species in four recovery-capacity classes absent from unburnt midstorey classes (sclerophyll and rainforest) compared to burnt (open midstorey) sites.

et al. 2008) and the modification of ectomycorrhizal communities (Horton *et al.* 2013). Harvest *et al.* (2008) found that surface root biomass increased by nearly 500% following rainforest encroachment of eucalypt forest in Tasmania. Such increases would place encroaching rainforest trees in direct competition with understorey plants for belowground resources, particularly on sites where seasonally high rainfall and shallow water tables force trees and graminoids to share similar rooting depths (Rossatto *et al.* 2014). Additionally, several rainforest pioneers, including *A. excelsa*, which was common in this study, have been shown to have a higher capacity to extract soil water than neighbouring eucalypts during severe water stress (Bowman *et al.* 1999). Indeed, consistent with the theory of multiple resource limitation (Chapin *et al.* 1987), limited water availability has been found to reduce plant shade tolerance and increase shade-induced plant mortality (Aranda *et al.* 2005; Valladares *et al.* 2016). However, there are little data on the belowground differences between these tree groups (Veldman *et al.* 2013), and the potential mechanisms need further study.

Similar across both unburnt treatments, high basal area of wattles also showed strong negative effects on understorey species richness and was likely a key driver of declines on unburnt sites without rainforest pioneers. Potential mechanisms of understorey decline beneath wattles include those associated with rainforest trees (increased competition for light, water and nutrients; increased litter fall), although nitrogen fixation by wattles may have an additional influence on understorey composition by modifying soil chemistry and nutrient profiles (May & Attiwill 2003). While we analysed wattles separately, the two species in our study share functional similarities to rainforest pioneer trees and could arguably fall within the ambit of rainforest encroachment. Like many rainforest pioneers, *A. disparrima* is associated with rainforest margins, and both species have seed morphologies indicating long-distance dispersal by birds, being presented in the canopy with coloured, bird-attracting funicles (O'Dowd & Gill 1986; Harden 1990). Such seed morphologies are common among wattles associated with rainforest margins, including *A. melanoxylon*, *A. maidenii* and *A. orites* and likely facilitate dispersal into adjacent open forests along with other rainforest pioneers.

The understorey declines observed in this study are ecologically important because understorey plants comprise the majority of plant diversity within open forests (Specht & Specht 1989, 1999; Valladares *et al.* 2016) and in this study included 83 ± 2.2% of species recorded in burnt sites. Of these, species losses to rainforest invasion were considerable for dry forest specialists (77.5%), graminoids (59.2%), shrubs (62.7%) and forbs (66.1%), demonstrating that even in the early stages of rainforest expansion, much of the site's original floristic diversity can be lost. Among dry forest understorey plants that endured rainforest invasion in this study, most have declined substantially in abundance, and generally occur as scattered, moribund individuals with few leaves (A. G. Baker, unpubl. data, 2018). Such populations are likely to continue to decline whether current conditions persist, and the results of this study are therefore likely to underestimate the full impact of continued fire exclusion and canopy closure.

Among plants killed by encroachment, we have identified several barriers to recovery that are likely

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to restrict the pool of species available for recolonisation and to prevent recovery of pre-encroachment floral communities. If fire were reintroduced to the system, recovery of standing plant populations would require long-lived seed banks or long-distance dispersal (Auld *et al.* 2000). In our study, 19% of displaced species had no capacity for recovery due to the absence of both a soil seed bank and wide dispersal capacity (wind, vertebrate dispersal). And for a further 68% of displaced species, recovery may be limited by the absence of one of these recovery mechanisms. Species with soil seed banks may persist until the return of fire (Auld *et al.* 2000; Auld & Ooi 2008), but not indefinitely. A study of seedbank longevity in comparable heathy dry forests near Sydney estimated that 'long-lived' seed banks may be typically exhausted only 1–2 decades after adults have died, with the plants becoming locally extinct if fire-free intervals exceeded this threshold (Auld *et al.* 2000). It is plausible that seedbank longevity may be further reduced by rainforest invasion, by premature shortening of adult contributions to soil seed banks (e.g. adult senescence, Keith 1996; suppressed flowering, Specht & Specht 1999) or accelerated fungal decay of seed banks (Mordecai 2012).

Species with transient seed banks (e.g. most species of Proteaceae, Myrtaceae) including canopy-stored become locally extinct with the death of adult plants (Keith 1996), with recolonisation only possible by long-distance dispersal. However, movement is critically limited for gravity- or ant-dispersed species (<10 m, Hughes & Westoby 1992; Hughes *et al.* 1994), effectively preventing recolonisation from remote populations following local extinction (Kirkman *et al.* 2004; Suding *et al.* 2004). Dispersal may be further restricted in highly fragmented landscapes if intervening habitat prevents gradual migration over multiple generations or movement of dispersing fauna, including landscapes fragmented by rainforest expansion itself (Andersen *et al.* 2006; Parr *et al.* 2007).

Perhaps, the most critical determinant of recovery is the likelihood of fire returning to the site at all, in order to restore appropriate environmental conditions to the understorey. The severe reduction of near-surface fuels (graminoids and shrubs) that we observed following rainforest invasion is likely to reduce community flammability. Indeed, displacement of grassy fuels by encroaching rainforest trees is a widely recognised critical threshold (e.g. fire suppression threshold, Hoffmann *et al.* 2012a) in persistent state switches from open to closed forest (Scheffer *et al.* 2001; Ratnam *et al.* 2011). Thus, diminished fuels together with fire-retardant microclimatic conditions associated with rainforest trees (reduced wind speed, increased fuel moisture; Little *et al.* 2012; Hoffmann *et al.* 2012a,b) are likely to reduce the probability and intensity of future fires in rainforest-encroached sites. Accordingly, the frequency and intensity of future fires may be too low to remove the encroaching rainforest canopy through crown scorch or radiant heat penetration of bark (Hoffmann *et al.* 2009). Further research is needed to test related flammability thresholds in rainforest-encroached open forests in eastern Australia.

A final obstacle to plants reliant on seed for recovery is post-fire competition from midstorey rainforest trees, with all rainforest species in this study are capable of resprouting after fire (OEH 2014). Resprouting utilises existing energy stores and root networks to quickly re-establish canopy cover above competing seedlings (Kauffman 1991; Bond & Midgley 2001; Williams *et al.* 2012), rapidly exerting competitive pressure for light, water and nutrients. Following top kill by fire, ground-level basal sprouts of rainforest trees in tropical savannas can re-establish a dense canopy at 4 m within two years (Kauffman 1991; Williams *et al.* 2012).

The strong relationship between fire exclusion, canopy closure and declining understorey plant diversity and density observed in the present study suggests that fire exclusion and rainforest expansion are major threats to understorey plant communities in open forests of eastern Australia. Recognition of the study ecosystem as a *threatened ecological community* (Subtropical Coastal Floodplain Forest, New South Wales Biodiversity Conservation Act 2016) and habitat for the nationally endangered *Rutidosis heterogama* (Commonwealth Environment Protection and Biodiversity Conservation Act 1999) provide explicit local-scale imperatives to prevent displacement of understorey plant communities. However, with rainforest invasion widely reported in fire-excluded open forests from northern Western Australia to Tasmania, we believe our findings are broadly applicable to open-forest biodiversity conservation throughout these regions.

The short fire interval (16 years) in which we observed plant species declines strongly contradicts the recommended *maximum* fire-intervals for heathy dry open forest in NSW (30 years) and Queensland (25 years) (Kenny *et al.* 2004; NPRSR 2013). The recommended maximum interval of Kenny *et al.* (2004) is based on total plant lifespan (adult + seed), but fails to consider the potential for adult lifespans to be considerably reduced by interspecific competition. Our results show that competition from increased tree cover can cause premature senescence of over 50% of understorey plant taxa in only 16 years since fire. We recommend that future fire-interval guidelines account for premature understorey decline from canopy closure and consider regional and local variations in plant growth resources (e.g. rainfall and soil nutrients), which govern canopy closure rates (Murphy & Bowman 2012; Hoffmann

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et al. 2012a). Our results suggest that on lands managed for the conservation of open-forest biodiversity, fires should occur with sufficient frequency to prevent tree cover from reaching a level where shade-intolerant species fail to thrive.

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AUTHOR CONTRIBUTIONS

Conceptualization; data curation; formal analysis; investigation; methodology; project administration; validation; visualization; writing-original draft: A.G.B. Conceptualization; methodology; supervision; validation; writing-review & editing: C.F.C. Conceptualization; formal analysis; methodology; supervision; validation; writing-review & editing: K.B. Conceptualization; methodology; supervision; validation; writing-review & editing: R.F.

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SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Appendix S1. Functional identity, frequency and abundance of midstorey plants.

Appendix S2. Growth form, seed bank, dispersal capability and habitat association of understorey plants.

Appendix S3. PERMANOVA summaries for understorey plant richness and composition.

Appendix S4. Marginal test results from distance-based linear model analysis.

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