Do frugivorous birds assist rainforest succession in weed dominated oldfield regrowth of subtropical Australia?

Wendy NEILAN, Carla P. CATTERALL, John KANOWSKI and Stephen MCKENNA

Rainforest Cooperative Research Centre and Faculty of Environmental Sciences, Griffith University, Nathan, Qld 4111, Australia.

Corresponding author: John Kanowski

Address: Faculty of Environmental Sciences, Griffith University, Nathan, Qld 4111, Australia.

email: J.Kanowski@griffith.edu.au.

ph +61 7 3735 3823; fax +61 7 3735 4209

Citation details:

Neilan, W., Catterall, C.P., Kanowski, J. and McKenna, S. (2006) Do frugivorous birds assist rainforest succession in weed dominated oldfield regrowth of subtropical Australia? *Biological Conservation* **129**, 393-407.

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Abstract

Exotic plants often form the first woody vegetation that grows on abandoned farmland. If this vegetation attracts vertebrate frugivores which disperse the seeds of native plants, then native plants may recruit to such oldfield sites. However, there is debate about the extent to which exotic vegetation assists or suppresses the regeneration of native plants, and about its effects on faunal biodiversity. These issues were investigated in subtropical eastern Australia, where rainforests were cleared for agriculture in the nineteenth century, and where regrowth dominated by camphor laurel (*Cinnamomum camphora*, an exotic, fleshy-fruited tree) has become common on former agricultural land. The study assessed the assemblages of frugivorous birds, and the recruitment of rainforest plants, at 24 patches of camphor laurel regrowth. The patches were used by nearly all frugivorous birds associated with subtropical rainforest. Many of these birds (16 of 34 species) are considered to have a medium to high potential to disperse the seeds of rainforest plants, and eight of these were abundant and widespread in regrowth patches. Of 208 recorded plant species, 181 were native to local rainforest. The ratio of native to exotic species was higher amongst tree recruits than adult trees, both for numbers of species and individuals. Among native tree recruits, 79% of 75 species, and 93% of 1928 individuals, were potentially dispersed by birds. These recruits included many late-successional species, and there were relatively more individuals of late-successional, bird-dispersed native species amongst recruits than adult trees. The species richness, but not the abundance, of both frugivorous birds and of bird-dispersed rainforest trees decreased with distance from major rainforest remnants. Camphor laurel regrowth provides habitat for rainforest birds and creates conditions suitable for the regeneration of native rainforest plants on abandoned farmland. Careful management of regrowth dominated by fleshy-fruited exotic invasive trees can provide an opportunity for broadscale reforestation in extensively-cleared landscapes.

Key words: reforestation, restoration, seed dispersal, succession, exotic, *Cinnamomum camphora*

1. Introduction

Deforestation is a global threat to biodiversity and ecosystem services (Dobson et al., 1997; Mooney et al., 2005). While considerable areas of cleared land have reverted to secondary forest, and there have been increasing efforts to reforest degraded land, the rate of deforestation still greatly exceeds the rate of reforestation (Lugo, 1997; Young, 2000). Large-scale reforestation is considered necessary to offset ecological degradation in extensively cleared tropical and subtropical landscapes (Brown and Lugo, 1994; Dobson et al., 1997; Parrotta et al., 1997b; Lamb, 1998; Chazdon, 2003).

If the duration and intensity of agricultural use have been limited, diverse secondary forest may regenerate naturally on abandoned land (Uhl et al., 1988; Ashton et al., 2001). However, after sustained agricultural production, soil seed banks become depleted, and the regeneration of native plants becomes dependent on seed dispersal from remnant forest (Hopkins and Graham, 1984; Parrotta et al., 1997b; Wunderle, 1997; Duncan and Chapman, 1999, 2002). Other barriers to regeneration in this situation include competition from pasture grasses and weeds, seed and seedling predation, changes to the physical, chemical and biological properties of soils, and ongoing disturbances, particularly fire (Hopkins, 1990; Aide et al., 1995; Parrotta et al., 1997b; Holl et al., 2000; Duncan and Chapman, 2002). Consequently, much abandoned land in former tropical forest landscapes is covered by depauperate grassland or scrub (Richards, 1996; Posada et al., 2000; Ashton et al., 2001). Furthermore, many of the regrowth forests that do occur in these landscapes are dominated by invasive exotic plants, since these are often the earliest colonisers of highly disturbed areas (D'Antonio and Meyerson, 2002; Lugo, 2004).

The management of 'weedy regrowth' (also termed 'new' or 'emerging' forests: Lugo and Helmer, 2004) poses a dilemma for ecologists and land managers. Traditionally, and often for good reason, managers have focussed on eradicating or containing the spread of introduced plants, particularly species with the potential to invade native vegetation (Ewel and Putz, 2004). However, weedy regrowth may provide important habitat for native wildlife (Zavaleta et al., 2001; D'Antonio and Meyerson, 2002; Moran et al., 2004a) and may also, over time, acquire a native flora, especially if there is frugivore-mediated dispersal of seeds from external sources (Wunderle, 1997; Aide et al., 2000; Williams and Karl, 2002; Erskine Ogden and Rejmanek, 2005). Resolution of the dilemma requires an understanding of seed dispersal and successional processes in a particular context. Most plant species in tropical and subtropical rainforests are fleshy-fruited and dispersed by vertebrates, especially birds (Howe and Smallwood, 1982; Willson et al. 1989), and birds can also be important dispersers in other ecosystems (Wunderle, 1997; Erskine Ogden and Rejmanek, 2005). Hence, a knowledge of how frugivorous birds use regrowth areas is important as a basis for understanding the potential of the regrowth to recruit a more diverse flora. However, few studies of vegetation development in oldfields have explicitly included a quantitative assessment of either the bird assemblage or the role of frugivore-mediated dispersal in community-level patterns of plant recruitment.

This paper assesses the potential for regeneration of native rainforest within regrowth vegetation dominated by an exotic tree species, camphor laurel (*Cinnamomum camphora*: Lauraceae), in oldfields of subtropical Australia. It also considers the use of this regrowth by frugivorous bird species, and their potential roles in seed dispersal. Camphor laurel, native to subtropical east Asia, is a large evergreen tree with aromatic leaves, wood and fruits. In eastern Australia, camphor laurel was widely planted as a shade and amenity tree after clearing. It typically produces prolific crops of black succulent fruits, 10 mm in diameter, over autumn and winter. The seeds of camphor laurel are primarily dispersed by birds, but may also may be spread by frugivorous bats (*Pteropus spp*.) and water (Firth, 1979; Date et al., 1991; Scanlon et al., 2000; Stansbury and Vivian-Smith, 2003).

Camphor laurel is considered an undesirable invasive plant in productive agricultural lands and some types of native forest, but it also provides food resources and other habitat for rainforest wildlife, and hence may contribute to regional conservation (Date et al., 1996; Scanlon et al., 2000). Seedlings of camphor laurel can recruit and persist in pasture (Wardell-Johnson et al., 2005), so that when farmland is abandoned or livestock grazing reduced, the rapidly-growing seedlings can quickly form a shrubland of abundant small individuals and then a developing forest patch as the trees grow and their canopies merge. Within a patch, the dense canopy of camphor laurel tends to shade out light-demanding pasture grass and herbs (Firth, 1979). However, longer-term successional processes within camphor laurel regrowth, including its potential to either assist or suppress the regeneration of native rainforest plants, are poorly known.

Specifically, this paper addresses the following questions: (1) To what extent are patches of camphor laurel regrowth used by frugivorous birds that are capable of dispersing rainforest plants? (2) How much regeneration of rainforest plants is occurring in these patches? (3) Do the use of camphor laurel patches by frugivores, and the regeneration of rainforest plants, vary with distance from remnant forest? The results are discussed in terms of the potential for regrowth that is dominated by invasive exotic plants to facilitate the broadscale regeneration of forest on cleared land, and the role of frugivorous fauna in this process.

2. Methods

2.1. Study region

The study was conducted near Lismore in subtropical north-east New South Wales, Australia (28^o 40' – 29^o S, 153^o 10' – 153^o 30' E). The study area comprises a basaltic plateau with an altitudinal range of 10 – 200 m a.s.l. and mean annual rainfall of 1 300 – 2 300 mm. Prior to European settlement, the plateau supported the 'Big Scrub', the largest tract of lowland subtropical rainforest in Australia (Floyd, 1990b). In the moist coastal parts of eastern Australia, the term 'rainforest' is used for a distinctive vegetation formation with a closed canopy, woody lianes, epiphytes, palms and strangler figs, and a diversity of tree species (typically including the Araucariaceae, Cunoniaceae, Elaeocarpaceae, Lauraceae, Meliaceae, Monimiaceae, Moraceae, Myrtaceae, Podocarpaceae, Proteaceae, Rutaceae, Sapindaceae, Sapotaceae and Sterculiaceae) (Webb et al., 1984; Floyd, 1990a; Kanowski et al., 2003). In the pre-European landscape, rainforest patches were set within a matrix of more open forest and woodland (dominated by *Eucalyptus* and *Acacia* spp.), from which they differ both structurally and floristically (Webb, 1968; Floyd, 1990a; Catterall et al., 2004).

The Big Scrub rainforest, estimated at 75 000 ha, was cleared to less than 1% of its original cover in the latter half of the nineteenth century (Frith, 1952, 1977; Floyd, 1990b). The three largest remnants (60 – 150 ha) are located at the northern limits of the former Big Scrub, contiguous with extensive moist eucalypt forests and upland rainforests of the Nightcap Range. There are approximately 30 smaller remnants (1-20 ha; most <5 ha) and scattered minor remnant patches and isolated trees elsewhere on the plateau (Floyd, 1990b). During much of the twentieth century, agriculture covered most of the region. Following declines in the dairy and banana industries since the 1960s, large areas reverted to regrowth dominated by camphor laurel (Firth, 1979). Aerial photographs (NSW Land and Property Information, 2002, 1:25000 Orthophoto map series) shows that 30 - 40% of the region is now covered with woody vegetation, about two-thirds of which is camphor laurel regrowth and the remainder plantations of macadamia (*Macadamia integrifolia* x *tetraphylla*) and other tree crops.

2.2. Study design

Twenty four patches of camphor laurel regrowth were surveyed in the region of the former Big Scrub rainforest, stratified by three zones of distance from the major remnants in the Nightcap Range: ‘close’ (seven sites; <1 km distant); intermediate or ‘mid’ (eight sites; 3-15 km) and ‘far’ (nine sites; 20-30 km, near the southern limit of the former Big Scrub). Sites were selected using aerial photography followed by ground-truthing and interviews with landholders. All sites were located on land that had been cleared of rainforest and had an intervening agricultural phase. Most sites had formerly been used for cattle pasture or banana plantations. The study focussed on the potential of established camphor laurel regrowth to support frugivorous birds and assist regeneration of rainforest plants, rather than on the succession of abandoned farmland to regrowth described by Firth (1979). Hence, for inclusion in the study, sites had to be comprised of regrowth at least 20 years old, with a tree stratum composed of >50% camphor laurel, and in a relatively advanced state of development (tree canopy >10 m high, foliage projective cover >50%, ground layer <30 % grasses and herbaceous weeds). Other selection criteria were that regeneration on the sites had occurred through natural process (i.e., not been facilitated by underplanting or poisoning of camphor laurel), and were at least 3 ha in size. At each site, a 0.6 ha plot was established and surveyed for frugivorous birds, floristic composition and forest structure.

2.3. Bird surveys

Each site was surveyed for birds on seven occasions. Four surveys were conducted between November 2003 and March 2004 (‘summer’) and three in May – June 2004 (‘winter’), the latter coinciding with the fruiting of camphor laurel. Summer and winter surveys were conducted by different observers. Each survey consisted of a 45 minute search of a 0.6 ha plot. Most surveys were conducted during the morning, and none were conducted during heavy rain or excessive heat. All birds seen or heard within a plot, or flying just above the canopy, were recorded.

Only frugivorous species are considered in this paper. Frugivorous birds were classified into functional groups based on their seed dispersal potential (high, medium, or low: adapted from Moran et al., 2004b). This classification reflects the amount of fruit in a bird’s diet, the width of its gape (which constrains the size of fruit it can consume), and whether it is likely to disperse viable seeds. Birds with ‘high’ seed dispersal potential are either large-gaped (>15 mm) and consume fruit at least regularly, or medium-gaped (10-15 mm) and consume fruit as a major component of the diet. Birds with ‘medium’ seed dispersal potential are the remaining medium- and small-gaped (<10 mm) species, which consume fruit more than occasionally. Both ‘high’ and ‘medium’ seed dispersal potential birds disperse viable seeds. The ‘low’ seed dispersal potential birds are those that consume fruit only occasionally and/ or those that destroy a high proportion of seeds in feeding or digestion.

2.4. Botanical surveys

All vascular plants >0.5 m tall were surveyed in five 50 m transects evenly spaced within each 0.6 ha plot. The width of each transect was 2 m for plants <2.5 cm d.b.h. (diameter 1.3 m above ground), 4 m for plants 2.5–10 cm d.b.h., and 10 m for larger size classes. To be counted, plants had to be rooted within the transect or, in the case of epiphytes, growing on a plant rooted in the transect. Plant species were classified by origin (local rainforest trees, local non-rainforest trees, or exotics), dispersal mode (bird-dispersed or other), and life form (trees: species >6 m high at maturity; shrubs: woody plants <6 m at maturity; vines; and other, including ferns, fern allies, herbs, sedges and grasses). Bird-dispersed plants were species with fleshy fruits, mostly drupes, berries or arillate seeds, that were potentially dispersed by the extant avifauna of the region.

To assess the recruitment of trees, the richest component of the flora, species were categorised by successional stage in rainforest regeneration, according to Kooyman (1996). Bird-dispersed trees were further categorised by diaspore size (the dimension, usually width, of the dispersal unit (fruit, arillate seed or naked seed) which limits ingestion and dispersal by birds: van der Pijl, 1982). For example, fruits with soft flesh able to be pecked open by most birds (e.g., figs) were categorised according to seed size, rather than fruit size. Diaspores were categorised in the same size classes used to categorise the gape width of frugivores: small (<10 mm), medium (10-15 mm) and large (>15 mm). Dispersal mode and diaspore size were determined by reference to published sources (Williams et al., 1984; Floyd, 1989; Cooper and Cooper, 1994; Hauser and Blok, 1998; Butler, 2003; Hyland et al., 2003) and unpublished data (S. McKenna, C. Moran, pers. comm.).

Each individual tree was categorised by reproductive stage. On the basis of the history of clearing and oldfield succession in the region (Frith, 1952, 1977; Firth, 1979) and information on each site, adult trees were considered to represent early regeneration following abandonment of agricultural activities, although a few individuals may have been remnant trees. Adult trees were determined from size class data, according to the size reached by each species at maturity. For species that attain the canopy on maturity, stems >20 cm d.b.h. were considered adults, while for mid-canopy species, stems >10 cm d.b.h. were considered adults. Recruits of both canopy and subcanopy trees were defined as individuals <2.5 cm d.b.h. (and >0.5 m tall). The 0.5 m lower height limit was chosen to focus on established recruits; it intentionally avoids young seedlings, which appear patchily in space and time, and typically suffer high rates of mortality (Hopkins, 1975; Connell et al. 1984).

2.5. Vegetation structure

Structural attributes including canopy cover and height, basal area, stem density, presence of special life forms, ground cover and woody debris were surveyed in five 5 m radius quadrats per site, based on the methodology in Kanowski et al. (2003).

2.6. Analyses

Analyses of structural attributes, bird assemblages and certain plant data focussed on examining variation with distance from the major rainforest remnants. Variations in structural data between distance zones (close, mid, far) were tested with ANOVA and LSD tests.

Differences in the abundances of frugivorous birds among the three distance zones and between seasons (summer, winter) were tested with repeated measures ANOVA. Dependent variables tested included log-transformed abundances for any species that was recorded at 10 or more sites, and the species richness and log-transformed total abundances within each of the three seed dispersal categories (high, mid, low). The seasonal abundance measure for each site was the average across the four summer or three winter visits. In the repeated measures design, ‘sites’ were subjects, ‘distance’ the between-subject factor and ‘season’ the within-subject factor. The distance effect was tested using the site (distance) error and the season and distance x season effects were tested using site (distance) x season error (Quinn and Keough, 2002). Where distance effects were significant, pairwise t-tests were performed on the least square means. Analyses were carried out using PROC GLM in the SAS ver. 8 statistical software package (SAS Institute Inc., 1999).

Differences in species richness and abundance of plants within functional categories (origin, dispersal mode, successional stage, diaspore size) between distance zones were tested with single-factor ANOVA, with *P* values determined by randomisation (Edgington, 1980). Randomisations were performed with 5 000 iterations using the programs PopTools (Hood, 2005) and Resampling Stats in Excel (Blank et al., 2001). Where distance effects were significant, pairwise t-tests were performed on the least square means (as above).

Data were pooled across all sites to examine differences between the attributes and species composition of adult trees and recruits. First, chi-squared tests of independence were used to examine differences between adult trees and recruits in the proportions of plant species and individuals belonging to the functional categories listed above. Second, randomisation procedures were used to test the following hypotheses: (1) that species of bird-dispersed trees had increased in relative abundance in the recruit cohort when compared with adult trees; and (2) that later-successional tree species had likewise increased amongst recruits. These tests used the functional groups of dispersal mode (bird-dispersed or other) and successional stage (pioneer/ early secondary or late secondary/ mature, analysed within each dispersal mode). For these analyses, to allow for differences in species richness between adult and recruit cohorts, all species of adults and recruits were first ranked in order of decreasing abundance, independently within each age class. Tied ranks were averaged. The test statistic was the difference between functional groups (e.g., bird-dispersed vs. non bird-dispersed) in the number of species which increased in rank abundance from adults to recruits. For each analysis, the probability of getting a difference greater or equal to that observed was determined by randomisation with 5000 iterations, as above.

3. Results

3.1. Structural attributes of regrowth patches

Camphor laurel was by far the most dominant tree in the regrowth patches surveyed in this study, on average comprising 80% of basal area, with other exotic species contributing 4% and native species 16% of basal area (Table 1). Regrowth patches were tall (average 25 m) with a moderately closed canopy (average 58%). Most patches consisted of a relatively dense stand of woody stems, particularly in the smaller size classes, and some small-diameter vines. The ground cover was mostly leaf litter, with patches of bare soil and rock, and abundant small diameter woody debris. Tree and shrub seedlings, and herbaceous exotic plants were a small component of ground cover, while other exotic and native herbs were less common. Few structural attributes varied with the distance of regrowth patches from major rainforest remnants.

<insert table 1>

3.2 Frugivorous birds

Thirty-four species of frugivorous birds were recorded during the study (Table 2). Sixteen species were considered to have a high or medium potential for dispersing the seeds of fleshy-fruited plants, and half of these species were recorded at the majority of sites. The most commonly recorded frugivores with high or medium seed dispersal potential were the topknot pigeon (*Lopholaimus antarcticus*), which foraged in large flocks during winter when camphor laurel was fruiting; the figbird (*Sphecotheres viridis*) and Lewin's honeyeater (*Meliphaga lewinii*), both also recorded in greater numbers during winter; and the silvereye (*Zosterops lateralis*). Less abundant, but recorded at nearly all sites, were the pied currawong (*Strepera graculina*) and rose-crowned fruit-dove (*Ptilinopus regina*). Seven of the 16 species with high or medium seed dispersal potential recorded in the study were rare to uncommon in surveys (i.e., recorded on five or fewer sites, and nowhere abundant), including the wompoo fruit-dove (*Ptilinopus magnificus*), the paradise riflebird (*Ptiloris paradiseus*) and the satin and regent bowerbirds (*Ptilonorhynchus violaceus* and *Sericulus chrysocephalus*).

<*insert table 2*>

There were more species and individuals of frugivores recorded in surveys of camphor laurel patches in winter than in summer, including frugivores with high and medium seed dispersal potential (Fig. 1). The responses of frugivores to distance from major rainforest remnants were more complex. There were more species of frugivores overall, and more frugivores of the high and low seed dispersal potential guilds, in sites close to the major rainforest remnants than more distant sites (Fig. 1). However, only birds in the low seed dispersal potential guild were also more abundant in close sites. There were few clear responses of abundance to distance from remnants at an individual species level (Table 2). Two species with low seed dispersal potential, the brown cuckoo-dove (*Macropygia amboinensis*) and white-headed pigeon (*Columba leucomela*), were most abundant in close sites throughout the surveys, while the silvereye (medium dispersal potential) showed the opposite pattern. More complex responses were shown by two frugivores with high seed dispersal potential, the topknot pigeon and rose-crowned fruit-dove. During summer, both species were most abundant in close sites, but in winter, when camphor laurel was fruiting, rose-crowned fruit-doves were more abundant in mid and far sites, while topknot pigeons were more abundant in mid sites (Table 2).

<*insert Figure 1*>

3.3. Plant recruitment

A total of 208 plant species were recorded in the camphor laurel patches including 181 species of local rainforest plants, four local non-rainforest species and 23 exotic plants. The remainder of this paper focuses mainly on the plant species recorded in the smallest size class (>0.5 m high, <2.5 cm d.b.h.), considered to represent recent (but established) regeneration at the sites. Of these small-sized plants, 90% of 163 species were from local rainforests (Table 3). However, most individual small-sized plants were exotics. The three most common species of small-sized plants were seedlings of camphor laurel and two shade-tolerant exotics, small-leaved privet (*Ligustrum sinense*), a shrub, and large-leaved privet (*L. lucidum*), a small tree.

The majority of species and individuals of small-sized native plants were potentially dispersed by birds: 77% of 146 species and 90% of 2929 individuals (Table 3). Among exotic plants, 65% of 17 species and 91% of 5193 individuals were potentially bird-dispersed. Amongst all native small-sized plants, tree recruits were the most frequent life form, comprising 51% of 146 species and 66% of 2929 individuals recorded. Native tree recruits were almost as abundant (1928 individuals, Table 3) as the recruits of exotic trees (2152). Amongst all exotic small-sized plants, shrubs were the most frequent life form.

<***insert table 3***>

Variation in plant recruitment with distance from rainforest remnants

The overall species richness and abundance of native small-sized plants did not vary with distance from major rainforest remnants (Table 4). On average, there were many more species of native than exotic small-sized plants recorded per site, across all life forms. However, exotics were more abundant overall, particularly at mid sites (Fig. 2). The richness of bird-dispersed native trees was highest in close sites, particularly species with medium-sized diaspores (Fig. 3, Table 4). Bird-dispersed native trees with small diaspores did not vary in richness with distance from major rainforest remnants, but were much more abundant in mid sites than elsewhere (Fig. 3, Table 4). Native trees with large diaspores were uncommon in the regrowth patches.

<***insert Fig. 2***>

<insert Fig. 3>

<***insert table 4*** >

Comparison of the attributes of adult trees and tree recruits

The proportion of native to exotic trees in the regrowth patches was greater among recruits than among adults, for both species and individuals. Natives comprised 97% of 77 species (Table 3) of tree recruits, compared with 85% of 59 adult tree species (χ^2 test of independence, P=0.01). Similarly, natives comprised 47% of 4080 individual tree recruits, compared with 25% of 2158 adult trees (P<0.0001). Only two exotic tree species were recorded as recruits, although they were both very common (camphor laurel 22%, large-leaved privet 31%, of all recruits). Both species also dominated the adult cohort (camphor laurel 66%, large-leaved privet 9%, of all adult individuals). Both are bird-dispersed species with small diaspores.

The proportion of individuals of native trees that were bird-dispersed was greater among recruits (93%) than among adults (84%) (Table 5). Most species of bird-dispersed native rainforest trees belonged to the late secondary or mature successional phases, for both adults (55%) and recruits (68%). However, most individuals belonged to the early secondary phase (adults 69%, recruits 61%). The proportion of individuals from late secondary or mature successional phases was greater among recruits (37%) than among adults (14%), coincident with a reduction in the proportion of individuals of pioneer species (Table 5). Most bird-dispersed native rainforest trees had small diaspores. The proportion of individuals with small diaspores was lower among recruits (79%) than adults (89%).

<insert Table 5>

Recruitment trends at the species level

Eight of the ten most abundant native trees in the adult size classes were early successional species (Fig. 4). However, only three of these species, *Guioa semiglauca, Mallotus philippensis* and *Pittosporum undulatum*, were also abundant as recruits. Several of the later successional tree species that were relatively abundant as recruits were rarely recorded as adult trees (Fig. 4). Among native tree species, there was a tendency for bird-dispersed species to be proportionately more abundant in the recruit cohort than in the adult cohort (Table 6). Among bird-dispersed native trees, later-successional species were proportionately more abundant among recruits than adults, whereas among non bird-dispersed species there was no such pattern (Table 6).

<insert Figure 4>

< *insert Table 6*>

4. Discussion

4.1. Rainforest succession and frugivorous birds in camphor laurel regrowth

Patches of camphor laurel regrowth in the Big Scrub region have recruited a wide variety of native rainforest plant species, whose relative abundance and diversity in the regrowth patches appear to be increasing over time. These trends can be inferred from the increased ratio of native to exotic plants, both in species richness and number of stems, and the increased abundance of bird-dispersed later successional species, among recruits compared with adult trees. Firth's (1979) study of a chronosequence of camphor laurel regrowth patches similarly found a marked increase in the number of native rainforest species recruited to older regrowth patches. These trends imply (i) the dispersal of the seeds of later successional rainforest plants from remnant forests to patches of camphor laurel regrowth; and (ii) the differential survival of seedlings of rainforest trees and camphor laurel in the regrowth patches, given the abundant seed production of camphor laurel in the study area (Firth, 1979; Stewart, 2000). Camphor laurel is relatively light-demanding, with seedlings subject to high mortality in the shade of a closed canopy (Dunphy, 1991; Stewart, 2000), whereas later-successional rainforest plants (and some exotic trees) are relatively shade-tolerant (Hopkins, 1975; Floyd, 1990a; Kooyman, 1996). A possible alternative outcome of this study could have been a finding that the ratio of native to exotic trees was lower among recruits than among adults, which would have supported the view that camphor laurel was suppressing the regeneration of native rainforest plants.

A strong argument can be made that camphor laurel is facilitating the recruitment of native rainforest plants to abandoned farmland in the study region. Unlike many native forest trees in Australia (Kooyman, 1996; Toh et al., 1999) and elsewhere (Aide et al., 1995, 2000; Holl et al., 2000; Posada et al., 2000; Ashton et al., 2001; Lugo, 2004), camphor laurel can successfully recruit in pasture and, if grazing pressure is reduced, grow rapidly amongst grasses to form a regrowth patch (Firth, 1979; Wardell-Johnson et al., 2005). Once established, camphor laurel regrowth develops a relatively complex forest structure, with a basal area comparable to that found in Australian subtropical rainforest and intermediate values for canopy cover and height (Kanowski et al., 2003). The moderately dense canopy cover and litter layer create shade and other physical conditions which suppress the growth of pasture grasses and herbaceous weeds, but are suitable for the germination and growth of rainforest plants (Kooyman, 1996; Gilmore, 1999). By comparison, no rainforest tree had recruited to pasture that had been abandoned for over two decades at a site 70 km to the north of the study region, where camphor laurel was not present, except under the canopies of isolated shrubs and trees (Toh et al., 1999).

The accumulation of a diverse range of rainforest plants within camphor laurel patches can be attributed to their use by numerous frugivorous birds, which are the main dispersers of rainforest plants in subtropical Australia (Willson et al., 1989; Green, 1993; Moran et al., 2004b). Most of the frugivorous birds associated with subtropical rainforest (Gosper, 1994; Moran et al., 2004b) were recorded in this study, and the majority of these are known to feed on the fruit of camphor laurel (Table 2). The abundant and reliable winter fruit crop produced by camphor laurel has been considered an important food resource for frugivorous birds in subtropical Australia, particularly given the widespread clearing of lowland rainforests (Innis, 1989; Date et al., 1991). However, frugivorous birds also made use of camphor laurel regrowth patches during summer, when most rainforest plants are fruiting (Innis, 1989;

Scanlon et al., 2000), and this may be particularly important for seed dispersal to regrowth patches.

Individual frugivore species are likely to vary in their contribution to seed dispersal, depending on their diet, abundance, and movement patterns. Among the more common birds, the topknot pigeon, figbird and pied currawong are abundant, large-gaped, eat fruit regularly, and move long-distances daily, and may regularly transport seed from the major rainforest remnants to distant regrowth (Firth, 1979; Date et al., 1991; Price et al., 1999; Moran et al., 2004b). The topknot pigeon may be particularly important, as it is known to consume a wide range of fruits (Innis, 1989; Moran et al., 2004b), and to move daily over tens of kilometres between the remnant forests of the Nightcap Range and distant camphor laurel regrowth (Frith, 1982; Gosper, 1994). Frugivorous bats (*Pteropus alecto* and *P. poliocephalus*) also eat camphor laurel fruits (Scanlon et al., 2000), consume a wide range of rainforest plants, and move long distances nightly (Eby, 1991, 1998), although bats are only likely to disperse small seeds over long distances (McConkey and Drake, 2002). Common avian seed-dispersers that move shorter distances on a daily basis (rose-crowned fruit-dove, Lewin's honeyeater and silvereye) could also regularly bring seeds into regrowth patches from isolated trees and small rainforest fragments, if these occur nearby (McDonald, 1999).

Elsewhere, large-gaped frugivores may become uncommon in secondary forests, leading to a scarcity of large-seeded plants amongst recruits (Wunderle, 1997; Corlett, 2002). Indeed, differential declines in frugivores capable of transporting large seeds is an emerging conservation issue for plant regeneration in rainforest fragments (Silva and Tabarelli, 2000; McConkey and Drake, 2002; Moran et al., 2004b). In the camphor laurel regrowth of the Big Scrub region, however, large-gaped species such as the topknot pigeon, figbird and pied currawong are ubiquitous and abundant. While large-seeded tree recruits were generally rare in the regrowth patches, the proportions of tree species within the three diaspore categories in this study (small 73%, medium 24%, large 3%, of 59 species present as recruits: Table 5) does not differ significantly from the proportions recorded during a recent survey of six Big Scrub rainforest remnants (small 73%, medium 18%, large 9%, of 251 species; χ^2 test of independence, P=0.27; the authors' unpublished data). It seems that the relative abundance of large and medium-gaped frugivorous birds in camphor laurel has maintained a potential for the dispersal of larger-seeded rainforest plants to regrowth sites.

4.2. Managing weedy regrowth for conservation outcomes

The management of camphor laurel regrowth is contentious. Current recommendations include both its strategic retention and management for conservation purposes in some areas, and its elimination from others (Gilmore, 1999; Scanlon et al., 2000). Its abundant winter fruit crop has been credited with rescuing some previously-declining rainforest pigeons from local extinction (Frith, 1982; Date et al., 1996), including the rose-crowned fruit-dove (listed as 'vulnerable' under the New South Wales Threatened Species Conservation Act 1995), which was recorded in 92% of the regrowth patches surveyed in the present study. The regrowth patches were also used by a number of other forest-dependent native bird species (H. Bower, C. Moran and the authors' unpublished data).

There has been a widespread tendency amongst conservation managers to seek to control or even eradicate exotic species (Zavaleta et al., 2001; Ewel and Putz, 2004), particularly species like camphor laurel which can dominate large areas of land. For example, there have been proposals to replace large areas of camphor laurel in northern New South Wales with short-rotation eucalypt plantations (Scanlon et al., 2000). However, such plantations have relatively low potential either as habitat for rainforest biota or as catalysts of rainforest regeneration in extensively cleared landscapes (Parrotta and Knowles, 1999; Kanowski et al., 2005). In contrast, the results of this study support the contention that, despite being an exotic species, camphor laurel can assist the recruitment of native rainforest plants over large areas of former agricultural land (Gilmore, 1999). Therefore, proposals for its broadscale eradication on environmental grounds need to be viewed with caution.

Management of 'new forests' has been suggested as a potential broadscale restoration strategy for tropical forests, especially in the Caribbean (Aide et al., 1995, 2000; Lugo and Helmer, 2004). In these forests, native and exotic plants may persist as novel assemblages (Lugo, 2004). Alternatively, many authors have advocated the establishment of timber plantations to catalyse regeneration of native plants on cleared land (Parrotta et al., 1997b; Lamb, 1998; Janzen, 2000; Ashton et al., 2001; Ewel and Putz, 2004). Another alternative is to directly replant a diverse range of native forest plants on cleared land (Kooyman, 1996; Lamb et al., 1997). In the study region, timber plantations typically comprise 1-10 species planted at 1 000 stems/ha, while 'restoration plantings' comprise 20-100 species planted at up to 6 000 stems/ha (Catterall et al., 2004). The establishment costs of these two options in 2000 were $4-8 000/ha and $20-25 000/ha respectively (Australian dollars; Catterall et al., 2004, 2005). Replanting the area currently occupied by camphor laurel regrowth in the Big Scrub region would have cost in the order of $100-400 million for timber plantations and restoration plantings, respectively. By comparison, the camphor laurel regrowth surveyed in this study had recruited native rainforest trees at an average density of 1 500 individuals/ha (similar to timber plantations), and a richness comparable to restoration plantings (75 species recruited to 1.2 ha) (Tables 3, 4). On this basis, managing camphor laurel regrowth may be a cost-effective means of broadscale reforestation for biodiversity outcomes in subtropical Australia.

Comparison of the richness and abundance of recruits with adult trees in the present study suggests that rainforest plant diversity could increase over time within regrowth patches. However, development rates are unknown and the course of succession uncertain. The long-lived camphor laurel overstorey may inhibit the growth of recruited rainforest trees for many decades (Firth, 1979; Scanlon et al., 2000), and recruits must compete with shade-tolerant exotics such as privets (*Ligustrum lucidum* and *L. sinense*), which numerically dominate the recruitment cohort. Strategic management intervention may be able to speed up or modify the succession of rainforest species to prevent long-term dominance by camphor laurel, privets and other exotics (such as through selective weed control or enrichment planting of dispersal-limited species: Scanlon et al., 2000; Woodford, 2000). Such intervention to 'guide' succession within emerging or new forests has also been advocated elsewhere (Aide et al., 2000; Lugo and Helmer, 2004). Experimental intervention, coupled with monitoring of outcomes for native flora and fauna, could provide useful new information to resolve current dilemmas for managing these forests, wherever multi-species complexes which incorporate both native and exotic plants are developing.

4.3. How can interactions between invasive plants and frugivores assist forest recovery?

Vertebrate frugivores are key participants in the process whereby exotic plants catalyse the development of more diverse forests on cleared land (Parrotta et al., 1997b; Wunderle, 1997). The willingness of some frugivores to visit reforested areas (irrespective of the origin of plant species which comprise these areas), together with their wide-ranging dispersal of seeds, make them effective agents in the recruitment of fleshy-fruited plants to reforested sites, including both plantations and regrowth dominated by exotic plants (Wunderle, 1997). This phenomenon has been observed by researchers elsewhere in Australia (Willson & Crome, 1989; Keenan et al., 1997), New Zealand (Williams & Karl, 2002), Africa (Chapman and

Chapman, 1996; Duncan and Chapman, 1999), Asia (Oberhauser, 1997; Corlett, 2002; Kaewkrom et al., 2005; Lee et al., 2005) and the Americas (Parrotta et al., 1997a; Aide et al., 2000; Janzen, 2000; Jones et al., 2004; Erskine Ogden and Rejmanek, 2005).

Many of these studies have examined recruitment under dry-fruited plant species. Where degraded land occurs close to remnant forest, the presence of plantations or scattered individuals of wind-dispersed trees, or even dead trees or tree-like structures may be sufficient to attract frugivorous seed-dispersers and greatly increase the recruitment of forest plants (Keenan et al., 1997; Wunderle, 1997; Toh et al., 1999; Holl et al., 2000). However, structural complexity alone may have limited effectiveness in attracting frugivorous animals across extensively-cleared landscapes (Wunderle, 1997; Kanowski et al., 2003). For example, in abandoned Puerto Rican canefields, plant species richness in regrowth dominated by a wind-dispersed, exotic species declined within 2 km of native forest (Chinea, 2002).

Revegetation in which fleshy-fruited plants are dominant should attract more frugivores over longer distances, because the vegetation would not only provide suitable habitat structure, but also food resources to offset the energy costs and other risks of longer-distance movement (Wunderle, 1997). For example, the present study found only moderate variation in both frugivore abundance and native plant recruitment (which was dominated by fleshy-fruited species) between camphor laurel regrowth patches that were close to major remnant forests and those 20-30 km distant. Where native vegetation is predominantly fleshy-fruited, as in the present study, this is a useful phenomenon. In other situations (e.g., where the native vegetation is predominantly dry-fruited), it may lead to a risk of further invasion by fleshy-fruited plants (Lake and Leishman, 2004). Therefore, management needs to be both context-specific and sensitive to the multiple ecological roles that fleshy-fruited exotic invasive plants play in extensively-cleared landscapes.

Vertebrate frugivores are often the facilitators of invasion by fleshy-fruited exotic plants, including camphor laurel (Stansbury and Vivian-Smith, 2003; Gosper et al., 2005). Plant-frugivore interactions present both an increased risk for future plant invasions and an increased potential for broadscale restoration of degraded land. Given the extent of disturbance in many human-dominated landscapes, it is unlikely that large-scale restoration of forest cover will be able to create either an entirely native species assemblage, or one which closely mimics any historical species-abundance pattern (Catterall et al., 2004; Lugo and Helmer, 2004). Self-organising processes involving the frugivore-assisted dispersal of fleshy-fruited plants pose new opportunities and challenges for both ecological restoration and weed management at large spatial scales.

Acknowledgements

Hank Bower and Cath Moran conducted two of the winter bird surveys. Scott Piper provided statistical advice and Peter Benson and Naima Fine assisted with data collection. Constructive comments on the manuscript were made by members of the Griffith University wildlife ecology discussion group, two referees and Denis Saunders. Thanks to the many landholders who provided access to research sites, and to local authorities and landcare groups for their assistance. Vegetation maps of the study area were provided by Byron and Lismore councils. The project was conducted under NSW NPWS scientific licence S11037. It was funded by the Rainforest Co-operative Research Centre, Griffith University Patience Thoms Honours Scholarship and the Norman Wettenhall Foundation.

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Legends To figures

Fig. 1. Species richness and abundance (mean, SE) of frugivorous birds in camphor laurel regrowth. Data from summer (shaded bars) and winter (unshaded) surveys, in three distance zones from major rainforest remnants (close < 1 km, mid 3-15 km, far >20 km, n = 7, 8 and 9, respectively). All frugivorous birds (a-b), frugivores with high (c-d), medium (e-f) and low (g-h) seed dispersal potential. Units are numbers per 45 minute survey of 0.6 ha. P values from two factor ANOVA are shown in each graph; S season, D distance, SxD interaction.

Fig. 2. Species richness and abundance (mean, SE) of small-sized (>0.5 m high, <2.5 cm d.b.h) native plants (closed bars) and exotic plants (open bars) recorded in camphor laurel regrowth. Sites are stratified by distance from major rainforest remnants (c = close <1 km, m = mid 3-15 km, f = far >20 km). Units are numbers per 0.05 ha.

Fig. 3. Species richness and abundance (mean, SE) of recruits (>0.5 m high, <2.5 cm d.b.h) of bird-dispersed native tree species in camphor laurel regrowth, according to (i) distance from major rainforest remnants (c = close <1km, m = mid 3-15 km, f = far >20 km), and (ii) diaspore size (shading within bars). Units are numbers per 0.05 ha.

Fig. 4. Relative abundances of the twenty most common native tree species recorded as adults and recruits in camphor laurel regrowth, pooled over 24 sites. Species are ranked in order of decreasing adult abundance. Total area sampled was 6 ha (0.25 ha/ site) for adults and 1.2 ha (0.05 ha/ site) for recruits. Open bars = early successional (pioneer, early secondary); closed bars = later successional (late secondary, mature phase).

List of species: 1 *Guioa semiglauca*; 2 *Mallotus philippensis*; 3 *Pittosporum undulatum*; 4 *Acacia melanoxylon*; 5 *Flindersia schottiana*[†]; 6 *Ficus fraseri*; **7 *Archontophoenix***

cunninghamiana; 8 *Alphitonia excelsa*; **9 *Toona ciliata***†; 10 *Pentaceras australis*†; 11 *Jagera pseudorhus*; **12 *Acmena smithii***; 13 *Commersonia bartramia*†; 14 *Mallotus discolor*; **15 *Macadamia tetraphylla***†; **16 *Dysoxylum mollissimum***; **17 *Elaeocarpus grandis***; 18 *Glochidion ferdinandi*; **19 *Cryptocarya glaucescens***; **20 *Castanospermum australe***†; **21 *Pararchidendron pruinosum***; 22 *Rhodamnia rubescens*; **23 *Endiandra pubens***†; **24 *Neolitsea australiensis***; **25 *Arytera distylis***; **26 *Neolitsea dealbata***; 27 *Diploglottis australis*; **28 *Cryptocarya obovata***; 29 *Synoum glandulosum*; **30 *Sarcopteryx stipata***; **31 *Cryptocarya triplinervis***; **32 *Dysoxylum rufum***. Note: later successional species are in bold font; all species except those marked with a cross (†) are bird-dispersed.

Table 1. Structural attributes of 24 patches of camphor laurel regrowth. ANOVA results (*df* 2, 23) show differences in attributes with distance from major rainforest remnants (c = close <1 km, m = mid 3-15 km, f = far >20 km).

Structural attribute		Mean (SE)	ANOVA *P*	Distance effect
Canopy height (m)		25 (1)	0.43	
Canopy cover (%)		58 (2)	0.66	
Basal area (m^2per ha)	Camphor	39.3 (2.8)	0.69	
	Exotic	1.9 (0.6)	0.28	
	Native	7.8 (1.2)	0.28	
Density of woody stems by height class (per ha)	0.5 – 2 m	3 620 (638)	0.031	c < m
	2 – 5 m	1 175 (234)	0.15	
	5 – 10 m	354 (32)	0.54	
	10 – 20 m	330 (30)	0.12	
	> 20 m	190 (19)	0.80	
Special life forms (frequency index 0-5)	Wiry vines*	3.5 (0.30)	0.63	
	Slender vines	1.9 (0.26)	0.45	
	Robust vines	1.4 (0.2)	0.68	
	Palms	1.4 (0.3)	0.001	c > m, f
	Scramblers	1.1 (0.2)	0.74	
Ground cover (%)	Litter	57 (2)	0.43	
	Soil	16 (2)	0.06	
	Rock	16 (2)	0.001	f > c, m
	Tree trunks	4 (0.6)	0.68	
	Woody debris	3 (0.6)	0.24	
	Seedlings	1 (0.3)	0.24	
	*Ageratina***	1 (0.3)	0.022	m > c, f
Woody debris (intercepts per 50 m by diameter class)	2.5 – 10 cm	23 (2)	0.53	
	10 – 20 cm	2 (0.2)	0.013	c > f
	>20 cm	0.5 (0.2)	0.11	

* Vines assessed in three stem diameter classes: wiry (<1 cm), slender (1–5 cm), robust (>5 cm).
** *A. adenophora* or *A. riparia* (Asteraceae): exotic scrambling herbs common in young camphor laurel regrowth (Firth, 1979).

Table 2. Frugivorous birds recorded from 24 patches of camphor laurel regrowth. ANOVA results show *P* values for differences in abundance with distance from major rainforest remnants (c = close <1 km, m = mid 3-15 km, f = far >20 km) and season of survey (s = summer, w = winter) for species recorded at 10 or more sites. Birds surveyed on seven, 45-minute visits to a 0.6 ha plot in each patch.

Guild[a]	Species	No. of sites	No. of birds Mean (SE)	Anova *P* Season[b]	Distance[b]	Season x Distance[c]
High seed-dispersal potential						
L1	*Wompoo fruit-dove *Ptilinopus magnificus*	3	0.02 (0.01)			
L1	*Topknot pigeon *Lopholaimus antarcticus*	15	3.51 (1.03)			0.005
L1	*Figbird *Sphecotheres viridis*	23	2.11 (0.43)	<0.0001 (w)	0.10	0.23
L1	Channel-billed cuckoo *Scythrops novaehollandiae*	1	0.01 (0.01)			
M1	*Rose-crowned fruit-dove *Ptilinopus regina*	22	0.46 (0.08)			0.04
L2	*Olive-backed oriole *Oriolus sagittatus*	5	0.05 (0.03)			
L2	*Pied currawong *Strepera graculina*	23	0.79 (0.09)	0.33	0.10	0.89
L2	Paradise riflebird *Ptiloris paradiseus*	1	0.01 (0.01)			
L2	*Green catbird *Ailuroedus crassirostris*	10	0.21 (0.08)			0.007
L2	*Satin bowerbird *Ptilonorhynchus violaceus*	4	0.04 (0.03)			
Medium seed-dispersal potential						
M2	*Lewin's honeyeater *Meliphaga lewinii*	24	2.26 (0.19)	0.005 (w)	0.21	0.93
M2	Barred cuckoo-shrike *Coracina lineata*	1	0.01 (0.01)			
M2	*Regent bowerbird *Sericulus chrysocephalus*	1	0.01 (0.01)			
S1	*Mistletoebird *Dicaeum hirundinaceum*	14	0.26 (0.06)	0.037 (s)	0.32	0.51
S2	Varied triller *Lalage leucomela*	13	0.15 (0.03)	0.80	0.65	0.11
S2	*Silvereye *Zosterops lateralis*	24	4.55 (0.48)	0.07	0.006 (m,f>c)	0.83
Low seed-dispersal potential						
3	Noisy friarbird *Philemon corniculatus*	3	0.04 (0.02)			
3	*Noisy miner *Manorina melanocephala*	1	0.02 (0.02)			
3	Scarlet honeyeater *Myzomela sanguinolenta*	2	0.01 (0.01)			
3	*Black-faced cuckoo-shrike *Coracina novaehollandiae*	3	0.03 (0.02)			

3	Grey butcherbird *Cracticus torquatus*	2	0.02 (0.01)			
3	*Australian magpie *Gymnorhina tibicen*	9	0.12 (0.04)			
3	*Torresian crow *Corvus orru*	16	0.28 (0.06)	0.003 (w)	0.58	0.08
4	*Australian brush turkey *Alectura lathami*	20	0.92 (0.27)	0.002 (s)	0.92	0.05
4	*White-headed pigeon *Columba leucomela*	20	1.20 (0.34)	0.94	0.003 (c>m,f)	0.74
4	Brown cuckoo-dove *Macropygia amboinensis*	17	0.31 (0.07)	0.66	0.033 (c>f)	0.25
4	*Emerald dove *Chalcophaps indica*	5	0.05 (0.03)			
4	Bar-shouldered dove *Geopelia humeralis*	4	0.02 (0.01)			
4	Wonga pigeon *Leucosarcia melanoleuca*	7	0.05 (0.02)			
4	Sulphur-crested cockatoo *Cacatua galerita*	1	0.01 (0.01)			
4	*Rainbow lorikeet *Trichoglossus haematodus*	1	0.03 (0.03)			
4	*Australian king-parrot *Alisterus scapularis*	11	0.14 (0.04)			0.0005
4	*Crimson rosella *Platycercus elegans*	3	0.09 (0.06)			
4	Eastern rosella *Platycercus eximius*	2	0.04 (0.02)			

[a] Guilds based on gape width and degree of frugivory (adapted from Moran et al., 2004b). Gape width categories: L > 15 mm, M 10-15 mm, S <10 mm. Degree of frugivory: 1 = fruit is dominant in the diet, 2 = fruit eaten more than occasionally, 3 = fruit rarely eaten, 4 = seeds destroyed during feeding or in gizzard. Nomenclature follows Christidis and Boles (1994).

[b] ANOVA main effects were only considered in the case of a non-significant interaction.

[c] Significant interactions as follows: topknot pigeons were most abundant at close sites in summer but at mid sites in winter; rose-crowned fruit doves were most abundant at close sites in summer but at mid and far sites in winter; green catbirds were most abundant at mid sites in summer; Australian king parrots were most abundant at close sites in summer.

* = species which have been recorded eating camphor laurel fruit (sources: Firth, 1979; Gosper, 1994; Woodford, 2000; C. Moran, unpublished data).

Table 3. Total species richness and abundance of small-sized plants recorded in 24 patches of camphor laurel regrowth. Total area sampled was 1.2 ha. Small-sized plants >0.5 m high, <2.5 cm d.b.h. See text for definitions of life forms and dispersal modes.

Plant category	Species			Individuals		
	Native	Exotic	Total	Native	Exotic	Total
All plants	146	17	163	2 929	5 193	8 122
Life form						
Tree	75	2	77	1 928	2 152	4 080
Shrub	24	9	33	304	2 569	2 873
Vine	40	3	43	628	12	640
Other	7	3	10	69	460	529
Dispersal mode						
Bird	113	11	124	2 622	4 725	7 347
Other animal	15	3	18	122	8	130
Non-zoochoric	18	3	21	185	460	645

Table 4. Average species richness and abundance of all small-sized plants in 24 patches of camphor laurel regrowth, according to origin, dispersal mode, life form and diaspore size. *P* values show ANOVA results for differences among three distance zones from major rainforest remnants (c = close <1 km, m = mid 3-15 km, f = far >20 km). Small-sized plants >0.5 m high, <2.5 cm d.b.h. Area sampled was 0.05 ha per patch.

Plant category	Species richness			Individuals		
	Mean	(SE)	*P*	Mean	(SE)	*P*
Exotic plants	4.9	(0.3)	0.022 (m>c)	216	(44)	0.006 (m>c,f)
Native plants	27	(1.6)	0.49	122	(14)	0.64
Bird dispersed native plants	22	(1.4)	0.36	109	(13)	0.52
Bird-dispersed native trees	12	(0.8)	0.048 (c>m,f)	75	(8.7)	0.07
Bird-dispersed native shrubs	4.5	(0.4)	0.24	11	(1.6)	0.06
Bird-dispersed native vines	5.9	(0.6)	0.76	22	(5.1)	0.20
Bird dispersed native trees diaspore <10 mm	8.8	(0.6)	0.16	59	(8.1)	0.002 (m>c,f)
Bird dispersed native trees diaspore 10-15 mm	2.5	(0.3)	0.020 (c>m,f)	15	(4.3)	0.24
Bird dispersed native trees diaspore >15 mm	0.1	(0.1)	0.61	0.2	(0.1)	0.44
Non bird-dispersed native trees	2.0	(0.3)	0.91	5.5	(1.2)	0.19

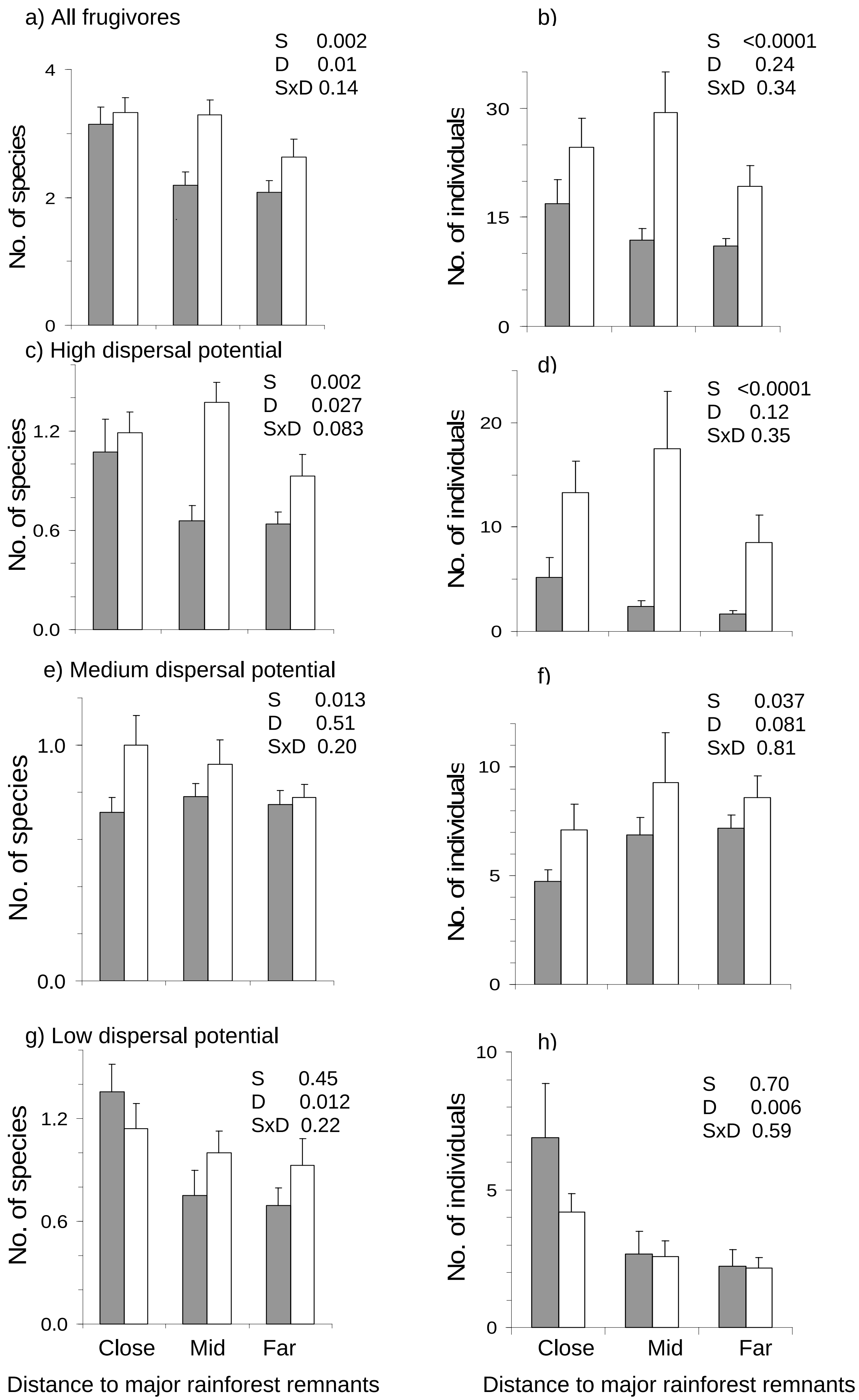
Table 5. Comparison of species richness and abundance of native rainforest tree species recorded as adults and recruits in 24 patches of camphor laurel regrowth, according to dispersal mode, successional stage and diaspore size. *P* values show results of chi-squared tests of independence of numbers of adults and recruits in each category. Total area sampled was 6 ha for adults and 1.2 ha for recruits.

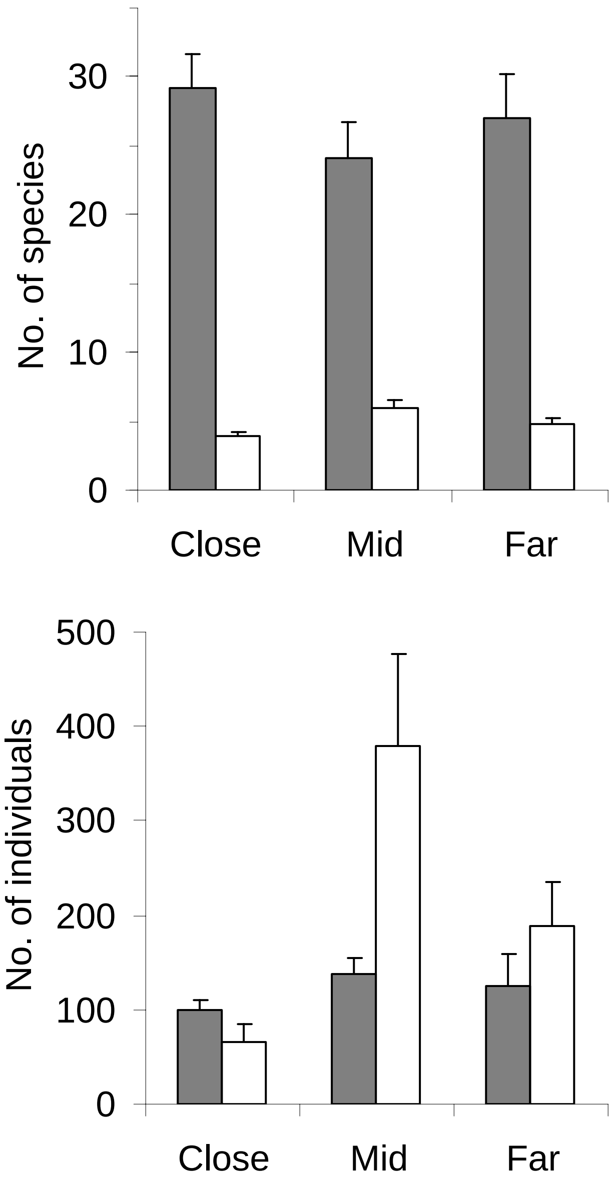
Plant category	Species		Individuals	
	Adult	Recruit	Adult	Recruit
All trees	50	75	541	1 928
All trees by dispersal mode				
Bird-dispersed	36 (72%)	59 (79%)	455 (84%)	1 796 (93%)
Non bird-dispersed	14 (28%)	16 (21%)	86 (16%)	132 (7%)
	$P=0.52$		$P<0.001$	
Bird-dispersed trees by successional stage				
Pioneer	6 (17%)	7 (12%)	76 (17%)	32 (2%)
Early secondary	10 (28%)	12 (20%)	314 (69%)	1 093 (61%)
Late secondary/ mature	20 (55%)	40 (68%)	65 (14%)	671 (37%)
	$P=0.49$		$P<0.001$	
Bird-dispersed trees by diaspore size				
Small (< 10 mm)	26 (72%)	43 (73%)	406 (89%)	1 423 (79%)
Medium (10 – 15 mm)	8 (22%)	14 (24%)	43 (10%)	369 (21%)
Large (> 15 mm)	2 (6%)	2 (3%)	6 (1%)	4 (0.2%)
	$P=0.87$		$P<0.001$	
Non bird-dispersed trees by successional stage				
Pioneer	1 (7%)	0 (0%)	10 (12%)	0 (0%)
Early secondary	2 (14%)	4 (25%)	38 (44%)	44 (33%)
Late secondary/ mature	11 (79%)	12 (75%)	38 (44%)	88 (67%)
	$P=0.45$		$P<0.001$	

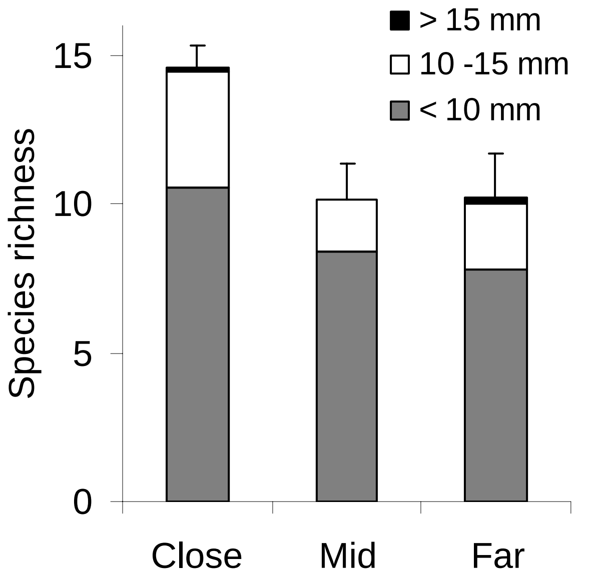
Table 6. Numbers of native rainforest tree species showing either an increase or a decrease in rank abundance between adult and recruit cohorts, in relation to dispersal mode and successional stage. *P* values show the results of randomisation tests comparing the number of species which increase in relative abundance from adults to recruits in each category. Data pooled across 24 patches of camphor laurel regrowth. Total area sampled was 6 ha for adults and 1.2 ha for recruits.

Category		Change in rank abundance from adults to recruits*	
		Decrease or no change	Increase
All native trees	Bird-dispersed	25	47
	Non bird-dispersed	11	9
		P=0.082	
Bird-dispersed	Early successional	11	10
	Later successional	14	37
		P=0.016	
Non bird-dispersed	Early successional	3	2
	Later successional	8	7
		P=0.77	

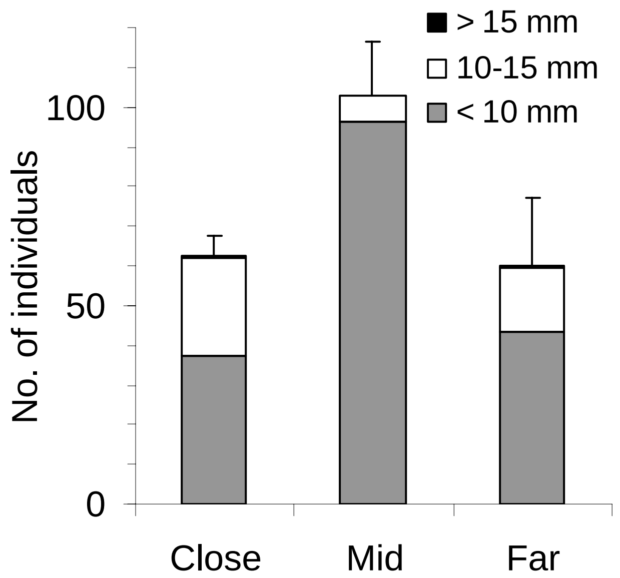
*An increase indicates that the species was relatively more abundant (lower rank) in the recruit cohort than in the adult cohort.


a) All frugivores
S 0.002
D 0.01
SxD 0.14
No. of species
0
2
4
b)
S <0.0001
D 0.24
SxD 0.34
No. of individuals
0
15
30
c) High dispersal potential
S 0.002
D 0.027
SxD 0.083
No. of species
0.0
0.6
1.2
d)
S <0.0001
D 0.12
SxD 0.35
No. of individuals
0
10
20
e) Medium dispersal potential
S 0.013
D 0.51
SxD 0.20
No. of species
0.0
1.0
f)
S 0.037
D 0.081
SxD 0.81
No. of individuals
0
5
10
g) Low dispersal potential
S 0.45
D 0.012
SxD 0.22
No. of species
0.0
0.6
1.2
h)
S 0.70
D 0.006
SxD 0.59
No. of individuals
0
5
10
Close
Mid
Far
Distance to major rainforest remnants
Close
Mid
Far
Distance to major rainforest remnants

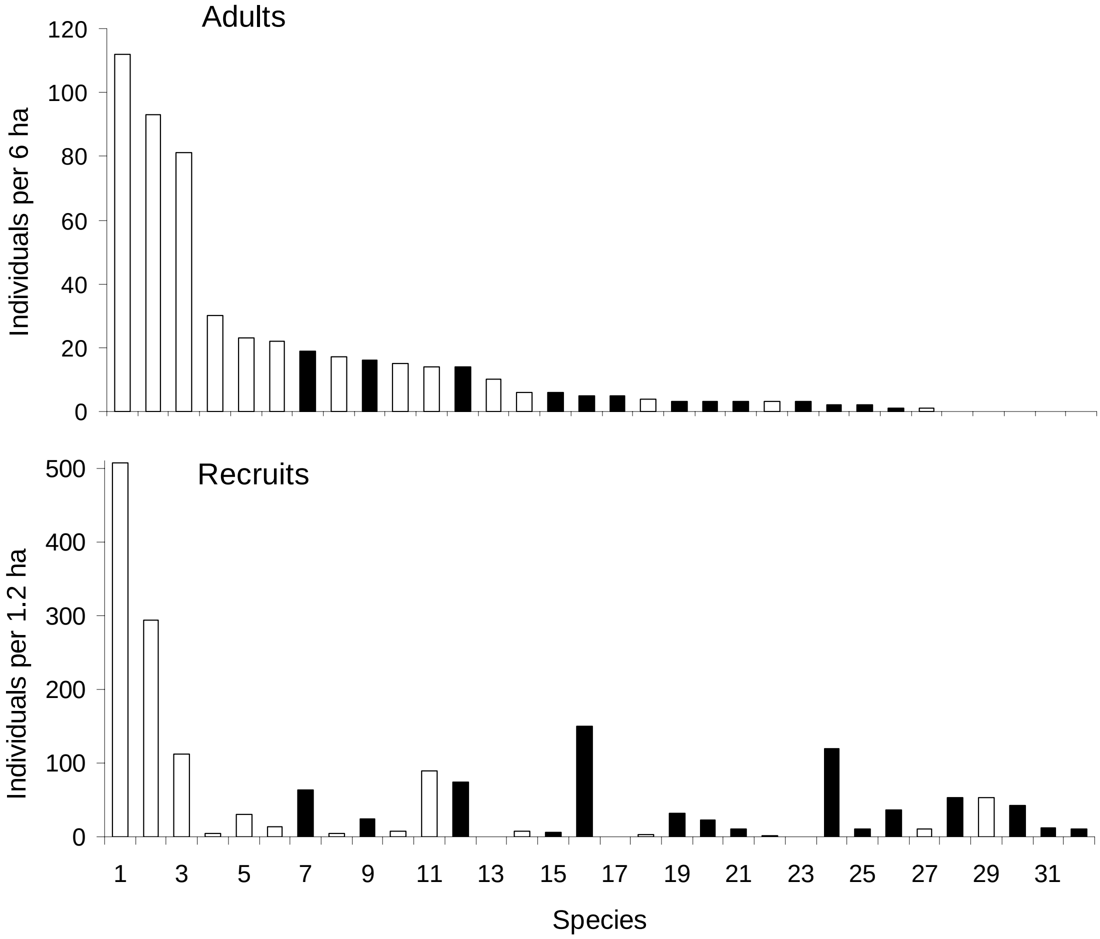

No. of species
0
10
20
30
Close
Mid
Far
No. of individuals
0
100
200
300
400
500
Close
Mid
Far



> 15 mm
10 -15 mm
< 10 mm
Species richness
0
5
10
15
Close
Mid
Far



> 15 mm
10-15 mm
< 10 mm
No. of individuals
0
50
100
Close
Mid
Far


Adults
Individuals per 6 ha
Recruits
Individuals per 1.2 ha
Species