

Silvicultural impacts in jarrah forest of Western Australia: synthesis, evaluation, and policy implications of the FORESTCHECK monitoring project of 2001–2006

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Summary

This paper, the final in a series of ten papers that report the impact of silvicultural treatments (harvesting and associated burning) in jarrah (*Eucalyptus marginata*) forest, reviews these papers and explores similarities and disparities. More than 2500 species were processed, dominated by macro-invertebrates, vascular flora and macrofungi. Few significant impacts were evident, and most species groups were resilient to the disturbances imposed. Regeneration stocking did not meet specified standards on two gap release and seven shelterwood grids subjected to silvicultural treatment in the period 1988–2002. Six treated grids had a retained basal area of more than 18 m² ha⁻¹, which obviated the need for further regeneration. More than 50 y may be needed for biological processes to reverse the increase in bulk density of soil caused during harvesting. Cryptogams (especially lichens) were the species group most sensitive to disturbance, although recovery of species richness was nearly complete 10 y after disturbance. For cryptogams and vascular flora, species recorded in only one grid (singletons) were more likely to occur on reference grids than on silviculturally treated grids. For all species groups studied, the imprint of harvesting 40 or more years earlier on species composition had become indistinguishable from that on grids never harvested. Soil nutrient status correlated with species richness for fungi on wood (negatively), light-trapped invertebrates (positively), birds (positively) and terrestrial vertebrates (frogs, reptiles and mammals, negatively). Silvicultural disturbance (timber harvesting and associated burning) correlated with species richness for fungi on wood (positively), terrestrial vertebrates (positively) and cryptogams (negatively). Time since the last (prescribed) fire did not correlate with any species group. Plant disease decreased species richness of light-trapped invertebrates by about 35%. Very few taxa were sufficiently widespread or sufficiently responsive to silvicultural disturbance to be of value as bio-indicators, demonstrating the superiority of biodiversity monitoring over bio-indicator monitoring. It is recommended that FORESTCHECK be expanded into a biological survey of the lower south-west of Western Australia.

Keywords: monitoring; reviews; silviculture; biodiversity; disturbed forests; disturbed soils; jarrah; Western Australia

Introduction

Disturbance is a term ultimately derived from Latin *turba*, crowd, connoting uproar, turmoil and confusion. By implication, in an ecological context, disturbance signifies any process that reduces the abundance of populations of one or more species by killing or removing individuals. The concept is of fundamental importance to the maintenance of biodiversity, and comprises both natural and anthropogenic processes (Attiwill 1994a,b). Natural disturbance occurs without any human intervention, and in south-west Western Australia (WA) includes lightning-caused fire, windstorm, flood and drought. Anthropogenic factors include human-ignited fire, timber harvesting, deforestation (for mining, farming, settlement), and pathogens, competitors and predators directly or indirectly introduced by humans (Dell *et al.* 1989).

The disturbance process in a forest caused by silvicultural treatment (felling, extraction and associated burning) can be analysed at any scale desired. During timber harvesting, trees are felled and the merchantable portion of the bole extracted to a landing where the logs are stacked before removal to a mill. The upper bole, branches and foliage remain where they fell. Later, a fire is set through the coupe in order to minimise unwanted fire during the years immediately following the commencement of regeneration, and to fertilise the soil and provide an ashbed in order to stimulate germination of plants and promote recolonisation by plants and fungi (Abbott and Loneragan 1986; Florence 1996). The risk that removal of vegetation may reduce shelter and exacerbate predation of native mammals by introduced foxes is reducible when poison baiting is implemented concurrently (Burrows and Christensen 2002). Any lapse in forest hygiene management may increase the spread of pathogens in soil (Shearer and Tippet 1989), with significant detriment to biodiversity (Cahill *et al.* 2008; Anderson *et al.* 2010).

Because most species in a defined area occur in small numbers, as demonstrated by dominance–diversity curves (Hubbell 2001; Magurran and Henderson 2003), there is a high risk that populations of highly localised sessile species could be obliterated by a fallen tree, by soil disturbance or by the post-timber harvesting fire (Burrows *et al.* 2001). The essence of ecologically

sustainable forest management is that affected species have the opportunity to recolonise harvested and burnt forest from adjacent unharvested, not recently harvested, unburnt or not recently burnt forest, or from seeds and spores already present in situ. Furthermore, a fairly orderly succession of species should ensue as their ecological requirements for nutrients, substrate, food, shelter or nest sites are satisfied (Attiwill 1994b).

FORESTCHECK is a project that retrospectively monitors the recovery of a variety of ecological processes and species groups after silvicultural disturbance (Abbott and Burrows 2004). In spring and the following autumn a particular forest ecosystem is sampled with about 10 grids differing in silvicultural disturbance (McCaw *et al.* 2011). External reference grids have either never been harvested or were last harvested for timber at least four decades previously, but all have been disturbed frequently by fire (McCaw *et al.* 2011). Shelterwood/selective cut grids were harvested so as to establish seedling regeneration beneath an overstorey of retained trees, and gap release grids were placed in forest patches up to 10 ha in area and harvested in order to reduce competition between overstorey and existing regeneration.

Although the design of FORESTCHECK does not allow for the explicit separation of the single effects of timber harvesting and post-harvesting burning, this is of little practical interest because both disturbances always occur together in jarrah forest.

Preceding papers in this special issue of *Australian Forestry* (Abbott *et al.* 2011; Cranfield *et al.* 2011; Farr *et al.* 2011; McCaw 2011; Robinson and Williams 2011; Ward *et al.* 2011; Wayne *et al.* 2011; Whitford and Mellican 2011) present a wealth of new information about the response of ecological processes and species across three kingdoms to modern silvicultural practices in jarrah forest in south-west WA. The focus of each of these papers is necessarily discipline-based. For this concluding paper all of the data collected in the period 2001–2006 were consolidated and analysed, and an interdisciplinary approach was pursued. The discoveries made in the preceding papers in this issue were identified and then compared, with special attention given to any inconsistencies and dissimilarities. The following questions were posed:

- How did total species richness (across all kingdoms) respond after silvicultural treatment?
- How extensive were changes in species composition and total abundance after silvicultural treatment?
- How important were stand structure (basal area), sub-regional location/year of study, and nutrient status in explaining the recovery of total species richness after silvicultural treatment?
- Is the biodiversity monitoring approach useful in comparison with more selective and focused bio-indicator monitoring?
- Based on the information presented in the preceding papers, as well as in this synthesis, what changes to policy and management practices and additional research are recommended?
- Were there any additional benefits of the FORESTCHECK monitoring approach that were not anticipated when the program was being planned?
- Were any lessons learnt that could be applied to assist those developing monitoring systems in other forests?

Methods

The statistical procedures applied are described in McCaw *et al.* (2011). In common with most of the studies, coupe buffers and external reference grids were combined into a single reference treatment. To facilitate comparisons between treatments, which differ slightly in numbers of grids, rarefaction was used to obtain valid comparisons (i.e. a common maximum sample size of 14 grids per treatment).

Statistical evidence is not cited in this paper when it has already been presented in the preceding papers published in this issue. Results of statistical analyses performed for this paper are, however, either summarised in table and figure captions or cited in the text. Simple correlation analyses were used to assess the relationships between species richness and total abundance with environmental factors.

Results

Tree regeneration, litter and woody debris accession, and soil compaction

Regeneration (as stocking) was variable, with most of the grids harvested for gap release satisfying the prescribed standards. However, few of those harvested as shelterwood achieved the specified regeneration stocking standard, and a number had retained basal areas greater than 18 m² ha⁻¹ which obviated the need for further regeneration. Replenishment of litter occurred within 5–10 y of silvicultural treatment, with the rate of accession dependent on forest cover. Coarse woody debris was greatest (as expected) in gap release grids (McCaw 2011). Tree basal area and forest cover declined with increased disturbance associated with timber harvesting, as did forest cover, with fire (Table 1).

Timber harvesting significantly increased the bulk density of surface soils. Although soil compaction increased as the intensity of disturbance activities increased, mean bulk density was not significantly greater in gap release grids compared to shelterwood grids. Nearly 12% of the harvest area had been disturbed by extraction tracks and landings. More than 50 y may be needed for biological processes to reverse the compaction of soil caused during timber harvesting (Whitford and Mellican 2011).

Response of group species richness to disturbance

The only species groups that showed significant differences between treatments were lichens (Cranfield *et al.* 2011) and terrestrial vertebrates (Wayne *et al.* 2011). The total number of lichens was lowest on gap release grids and intermediate on shelterwood/selective cut grids relative to the reference grids. By c. 10 y after disturbance, however, these differences had moderated and no statistical differences were evident. The total number of terrestrial vertebrates was greater on the shelterwood/selective cut grids relative to the reference grids.

The species accumulation graphs and dominance–diversity curves in each of the preceding papers showed few notable differences between treatments, except for cryptogams. All

Table 1. Inter-correlations between soil nutrients (N, P-total and P-extractable, K-total and K-extractable; tot = total, ex = extractable; PC1 = first principal component extracted from the correlation matrix between soil nutrients), disturbance (Dist. (log)) due to silvicultural treatment (= timber harvesting and associated fire), disturbance (Dist. (fire)) due to planned fire (fire not associated with timber harvesting) scaled from 0 to 1 based on number of years less than 10 since last planned fire), forest cover and basal area. Values followed by * are significant at $P < 0.05$; critical values are $r > 0.3$, $P < 0.05$; $r > 0.5$, $P < 0.01$, approximately.

Variable	N	P (tot)	P (ex)	K (tot)	K (ex)	PC1	Dist. (log)	Dist. (fire)	Forest cover
P (tot)	0.51*								
P (ex)	0.30*	0.62*							
K (tot)	0.26	0.47*	0.25						
K (ex)	0.64*	0.67*	0.33*	0.61*					
PC1	0.95*	0.44*	0.10	0.11	0.67*				
Dist. (log)	-0.24	-0.09	-0.17	-0.12	-0.15	-0.18			
Dist. (fire)	0.29*	0.19	0.25	0.04	0.26	0.28	-0.06		
Forest cover	0.07*	-0.03	0.03	-0.08	-0.06	0.05	-0.52*	-0.28*	
Basal area	-0.02	0.06	0.19	-0.08	0.03	-0.02	-0.61*	0.14	0.52*

dominance–diversity curves showed that most species occurred at low abundance.

Response of total species richness to disturbance

When observed species richness across all biota was rarefied to the common level of 14 grids per treatment, there was little difference between the two silvicultural treatments and reference treatment in species richness (Fig. 1). However, when total species richness was estimated by extrapolating the species accumulation curves (to their asymptotes), reference grids were predicted to support

more species than shelterwood/selective cut and gap release treatments (Fig. 2). This is due to the higher number of singleton species (i.e. species recorded on only one grid) in reference grids. Cryptogams, vascular flora, macrofungi and birds showed significant change in predicted species richness in grids disturbed by silvicultural treatment relative to reference grids (Table 2). Macrofungal species richness increased on gap release grids, whereas cryptogams decreased on gap release grids and vascular flora and birds decreased on shelterwood/selective cut grids.

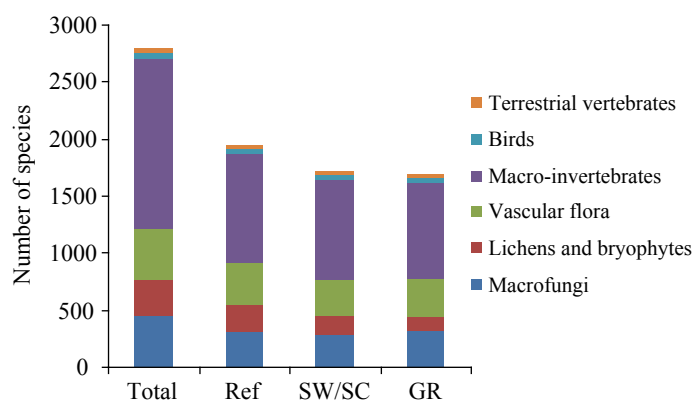


Figure 1. Observed species richness, rarefied to a common set of 14 grids, for reference (Ref), shelterwood/selective cut (SW/SC) and gap release (GR) treatments.

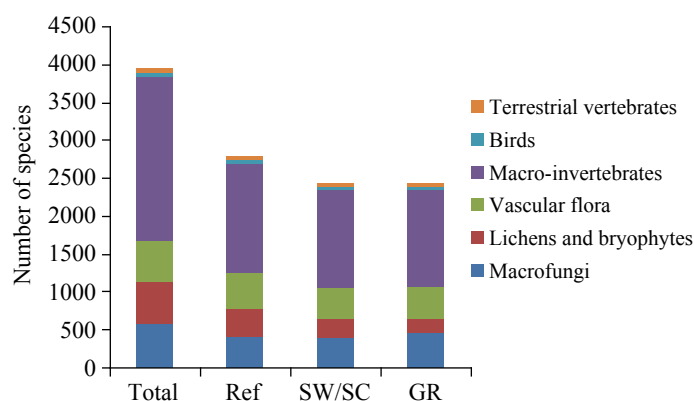


Figure 2. Predicted species richness for reference (Ref), shelterwood/selective cut (SW/SC) and gap release (GR) treatments.

Table 2. Changes (%) in predicted richness and singleton species (rarefied), relative to the reference treatment ($n = 14$). Values followed by * are significant at $P < 0.05$; only cryptogams have $P < 0.01$.

Attribute	Treatment	Macrofungi	Cryptogams	Vascular flora	Macro-invertebrates	Birds	Terrestrial vertebrates	Total
Richness	Shelterwood	-6.6	-25.0*	-19.8*	-8.7	-19.1*	-20.5	-12.7
	Gap	7.8*	-44.9*	-11.9	-11.3	-8.0	-16.5	-12.8
Singletons	Shelterwood	8.0	-8.1	-20.8*	0.8	-21.8	-32.8	-4.2
	Gap	27.4*	-34.9*	-6.2	2.8	12.8	-41.5	-3.3

Differences between silvicultural treatments in the number of singleton species rarefied to 14 sites are shown in Fig. 3. Differences relative to the reference grids are presented in Table 2. The number of singleton species relative to the reference grids increased on the gap release grids for macrofungi ($P = 0.041$), decreased on the gap release grids for cryptogams ($P = 0.000$) and decreased on the shelterwood/selective cut grids for vascular flora ($P = 0.022$).

For macrofungi, 69 species were restricted to reference grids while 35 were restricted to shelterwood/selective cut and 62 to gap release treatment. For cryptogams, the number of singleton species was 41 and 28 in the shelterwood/selective cut and gap release grids respectively, considerably less than the 78 recorded in the reference grids. This difference is even more accentuated when calculated on the basis of treatment, with 100, 44 and 27 species of cryptogams restricted to reference, shelterwood/selective cut and gap release treatments respectively, though these are not rarefied or combined. For vascular flora, more species were recorded as singletons or with low frequency in reference grids compared to silvicultural treatments.

For the animal groups sampled, the greater estimates of richness of macro-invertebrates in reference forest are attributable to a greater proportion of macro-invertebrate species from single-sample grids. All five bird species recorded as singletons were not associated with any one treatment. Eight species of terrestrial vertebrates were recorded as singletons; seven were associated with reference grids (one, three and three species each at a coupe buffer, external reference and never-harvested grid, respectively) and one snake species *Notechis scutatus* recorded at a shelterwood grid. Except for the eight singletons and the frog species *Pseudophryne guentheri* (two records), no species was detected exclusively within one treatment class.

Response of total abundance to disturbance

No statistically significant difference between treatments was detected for vascular flora, macrofungi and terrestrial vertebrates. This may in part have resulted from the underlying clumped distribution of abundances of the component species. Although the vascular flora showed a progressive decrease with time since disturbance, this trend was not statistically significant. When

the analysis was rarefied across all groups (except cryptogams, for which abundance data were not recorded), more individual organisms were recorded in disturbed treatments than in reference forest.

Species compositional changes following disturbance

For all groups studied, species assemblages on reference grids harvested more than 40 y previously converged with those on reference grids that had never been harvested. This implies that the imprint of previous silvicultural treatment had become indistinct at the community level by c. 50 y.

Assemblages of birds and terrestrial vertebrates showed no differences, and vascular flora showed only weak differentiation, between disturbed grids and reference grids. Cryptogam and macrofungal species assemblages on shelterwood/selective cut and gap release grids were equally distinct from those on reference grids, although cryptogams on one of each of the disturbed grids aligned more closely with the reference grids. Macrofungal assemblages were most distinctive on grids sampled 1–4 y since treatment but this difference moderated on grids sampled 5–9 y and more than 10 y since treatment.

Influence of ecosystem/year of study on species composition

All biota groups showed distinct regional or year-of-sampling effects. Five separate groupings of grids were evident for cryptogams and macro-invertebrates, four for macrofungi, birds and terrestrial vertebrates, and three for vascular flora. Where overlap occurred, there was no consistency between the biota groups.

Influence of nutrient status, disturbance and basal area on total species richness and abundance

Inter-correlations between soil nutrients (N, P-total and P-extractable, K-total and K-extractable) and disturbance due to silvicultural treatment (fraction of basal area of jarrah and marri removed at harvest), burning (disturbance (fire), scaled from 0 to 1 based on the number of years less than ten since last fire), current basal area, and forest cover were examined. Significant positive inter-correlations were found between soil nutrients (eight of ten comparisons), but only weak or no relationships between soil nutrients and disturbance were apparent (one of ten; Table 1).

Correlations of measures of soil nutrient status, disturbance due to silvicultural treatment, disturbance due to planned fire not associated with harvesting, basal area and forest cover with species richness and total abundance are summarised in Table 3. For the strongest relationship, species richness and total abundance of invertebrates (light-trapped) both increased in relation to the levels of extractable K in soil (Fig. 4). Note, however, that nine sites with extractable soil K greater than 100 mg kg⁻¹ of soil were all from one region (Jarrah North East, grids FC28–FC37) surveyed in spring 2004 and autumn 2005.

Because the soil nutrient data were strongly inter-correlated, the first principal component was extracted in order to obtain a single 'productivity' axis. Disturbance due to silvicultural treatment was calculated as the fraction of jarrah and marri removed; and disturbance (prescribed fire) was scaled from 0 to 1, based on the

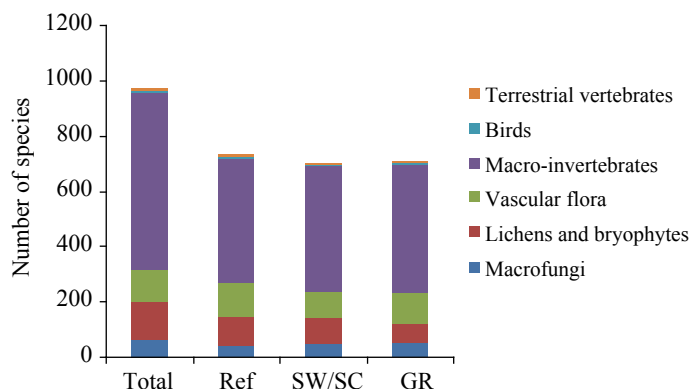


Figure 3. The number of singleton species (i.e. recorded at only one grid), rarefied to a common set of 14 grids, for reference (Ref), shelterwood/selective cut (SW/SC) and gap release (GR) treatments.

Table 3. Correlations of species richness and total abundance with soil nutrients (tot = total, ex = extractable; PC1 = first principal component extracted from the correlation matrix between soil nutrients), disturbance (Dist. (log)) due to silvicultural treatment (= timber harvesting and associated fire), disturbance (Dist. (fire)) due to planned fire (= fire not associated with timber harvesting), forest cover, and basal area. Values followed by * are significant at $P < 0.05$; critical values are $r > 0.3$, $P < 0.05$; $r > 0.4$, $P < 0.01$, approximately.

Species group	Attribute	N	P (tot)	P (ex)	K (tot)	K (ex)	PC1	Dist. (log)	Dist. (fire)	Forest cover	Basal area
Birds	Richness	0.01	0.36*	0.41*	0.14	0.06	0.27	0.07	-0.13	0.15	0.01
	Abundance	0.00	0.38*	0.44*	-0.03	-0.06	0.15	0.13	-0.02	0.07	0.02
Invertebrates (light trapped)	Richness	-0.02	0.11	-0.05	0.46*	0.34*	0.34*	0.13	0.06	-0.09	-0.08
	Abundance	0.44*	0.44*	0.06	0.67*	0.68*	0.70*	-0.07	0.02	-0.11	-0.16
Vertebrates	Richness	-0.29*	-0.22	-0.22	-0.38*	-0.26	-0.32*	0.33*	-0.16	-0.07	-0.13
	Abundance	-0.12	-0.10	-0.06	-0.27	-0.09	-0.15	0.20	-0.12	0.07	0.03
Fungi (soil)	Richness	-0.02	0.08	-0.10	-0.12	0.02	-0.04	0.24	0.17	-0.15	-0.12
	Abundance	0.13	0.18	0.05	-0.04	0.18	0.09	0.34*	0.30*	-0.28	-0.23
Fungi (litter)	Richness	0.10	0.25	0.02	0.06	0.24	0.17	-0.04	0.13	0.00	0.06
	Abundance	0.39*	0.35*	0.28	0.10	0.21	0.28	-0.36*	-0.09	0.22	0.15
Fungi (wood)	Richness	-0.07	-0.13	-0.19	-0.47*	-0.20	-0.34*	0.38*	0.21	-0.30*	-0.10
	Abundance	-0.09	-0.01	-0.08	-0.25	-0.08	-0.14	0.44*	0.13	-0.37*	-0.15
Fungi (total)	Richness	-0.02	0.07	-0.12	-0.20	0.01	-0.09	0.27	0.20	-0.19	-0.11
	Abundance	0.14	0.21	0.07	-0.13	0.13	0.07	0.37*	0.25	-0.33*	-0.20
Cryptogams	Richness	0.15	0.19	0.28	0.06	-0.04	0.02	-0.50*	-0.26	-0.02	0.43*
Plants	Richness	-0.05	0.02	-0.03	0.11	-0.08	0.12	-0.06	-0.05	0.48*	-0.05

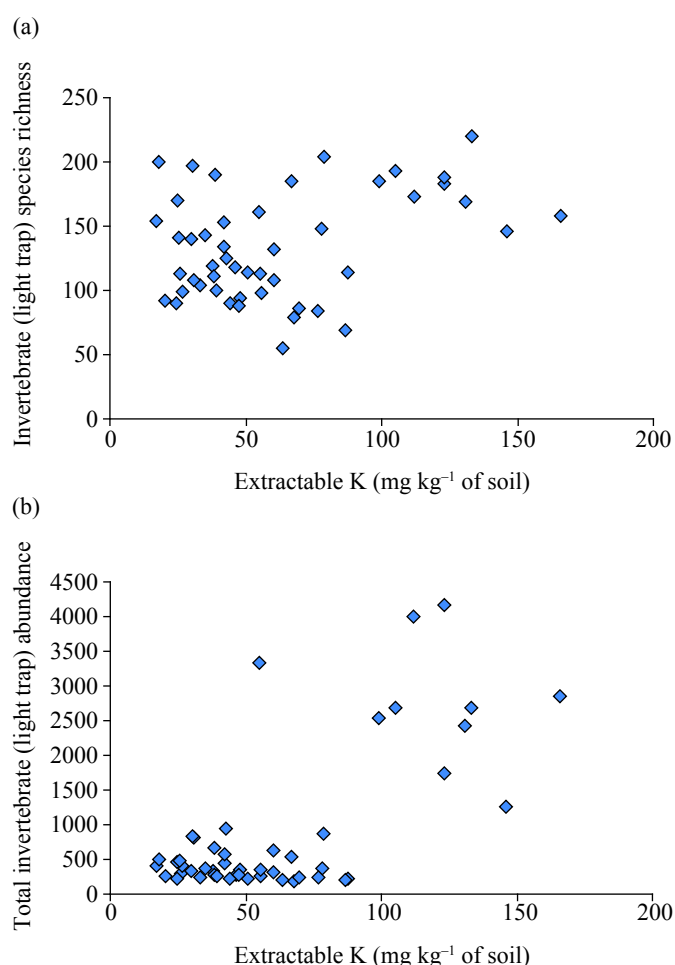


Figure 4. Species richness (a) and total abundance (b) of macro-invertebrates captured in light-traps in relation to extractable soil K. $r = 0.34$ ($P < 0.05$), $r = 0.68$ ($P < 0.01$), respectively.

number of years less than ten since the last fire. An additional measure of disturbance due to plant disease was assessed on only 42 grids (as presence/absence of dieback caused by the water mould *Phytophthora cinnamomi*, McCaw 2011) and differences assessed by *t*-test.

The nutrient and disturbance factors were related to richness and abundance (Table 3). The strongest response was shown by cryptogam richness, which declined with increased intensity of silvicultural treatment and, conversely, increased with foliage cover. Richness and abundance of macrofungi recorded on soil and wood increased with harvesting disturbance, but that recorded on litter decreased. Species richness of light-trapped invertebrates was significantly greater on sites without plant disease (mean 142 cf. 93 species, $P < 0.001$; other results not shown).

Influence of other environmental factors on the abundance of particular species

Information about soil nutrients, foliar nutrients, fox predation (on unbaited grids), forest cover and the proportion of marri present was either collected on or derived for each grid. For species that are sufficiently widespread or abundant, the possible influence of these factors can be explored by correlating with abundance of the commoner species on each grid. However, few significant and ecologically sensible correlations were evident.

The abundance of the partially folivorous *Trichosurus vulpecula* (koomal or brushtail possum) correlated significantly with foliar P and foliar K of jarrah ($r = 0.40$, $P = 0.005$; $r = 0.39$, $P = 0.006$, respectively), but not with foliar N in jarrah or with foliar N, P or K in marri. Koomal had much greater mean abundance on grids that were baited for foxes than on unbaited grids (mean 9.46 cf. 0.27, $P = 0.0002$), consistent with the fact that they are

not confined to the overstorey when feeding. The abundance of *Bettongia penicillata* (woylie) was also greater on baited than unbaited grids (3.50 cf. 0.14, $P = 0.02$). The woylie is a cursorial species with no effective shelter from foxes.

All of the significant correlations found between bird species and foliage nutrients (data not presented) had no compelling ecological basis. Moreover, most had low coefficients of determination (<0.2).

Surrogacy: how representative are bio-indicators as a substitute for total species richness?

Only three species of vascular flora and one macrofungal taxon occurred on all 48 grids. No cryptogams, macro-invertebrates, birds or terrestrial vertebrates occurred on all 48 grids. The information available for vascular flora is instructive, with 125 species exclusive to a single treatment and only 244 species (55%) recorded in all three treatments (Ward *et al.* 2011). Furthermore, 187 species were restricted to a single forest ecosystem/year of sampling, and only 61 species (14%) were recorded in all forest ecosystems/years of sampling. One hundred and one species were recorded on only one grid. For macrofungi, 141 species were recorded on only one of the 48 grids; 58, 33 and 50 within reference, shelterwood/selective cut and gap release treatments respectively. Comparable data for macro-invertebrates species recorded on only one grid were 670 species in total, including 508, 470 and 458 within reference, shelterwood/selective cut and gap release treatments respectively.

Top-order predators are often regarded as indicators of a stable ecological pyramid. Raptors, however, were in very low numbers and it was not possible to examine whether the abundance of raptors is an accurate predictor of total abundance of bird species. Lizard abundance (all species) did not correlate significantly with the abundance of pitfall-trapped invertebrates, total invertebrate species richness or total abundance of invertebrates. Species richness of spiders did correlate significantly with species richness of all other invertebrates ($r = 0.43$, $P < 0.05$), but the number of spider species was not large (0–10 species per grid, average of 4.2).

In Australia, the introduced *Mus musculus* (house mouse) is an indicator of greatly disturbed sites (Singleton 2008). Because only nine individuals were trapped, from four grids, it was not possible to examine its value as an indicator of disturbance in jarrah forest.

As possible indicator species, we arbitrarily selected those taxa occurring on more than 80% of grids (i.e. on more than 40 of 48) and related their abundance to 18 measures including soil (5) and foliar nutrients (6), forest cover, total basal area, silvicultural treatment and other measures of disturbance (presence of dieback and fox baiting), and the basal area and relative abundance of marri. This procedure resulted in the selection of 12 taxa—three bird, six invertebrate and three fungus species (abundance data were not consistently recorded for vascular flora and cryptogams, and no vertebrates occurred in over 40 sites). For total basal area, the basal area and relative abundance of marri, and disturbance due to fox baiting, or dieback, there were few statistically significant relationships (4 of 60 comparisons, roughly equal to the three (0.05×60) that would be expected by chance alone).

However, for soil and foliar nutrients, and for the two correlated measures of disturbance due to silviculture (fraction of basal area removed and forest cover), 34 of 156 relationships were significant, considerably more than the eight expected by chance alone. Most had significantly increased abundances on sites with greater fertility (25 increases cf. 4 declines), and on sites with increased disturbance due to silvicultural treatment (4 increases cf. 1 decline, Table 4).

Discussion

Fundamental causes of species richness patterns and species abundance in jarrah forest

Typical of most regions of Australia, taxonomic and biogeographic knowledge of the fish, amphibian, reptile, bird and mammal fauna of the jarrah forest is virtually complete. Knowledge of the vascular and cryptogamic flora is less complete. In contrast, knowledge of invertebrates and fungi is rudimentary, although improving. As a result, species richness gradients are well established for vertebrates (Abbott 1998, 1999), incomplete for vascular flora (Commonwealth and Western Australian Regional Forest Agreement (RFA) Steering Committee 1998: Map 5; Gioia and Pigott 2000), and poorly understood for cryptogams, fungi and invertebrates (except butterflies and termites, Abbott 1998). Moreover, these gradients show low geographical congruence between species groups (Abbott 1998, 1999; Abbott and Burrows 1999).

A complementary approach to understanding species richness is less empirical. In the theory proposed by Huston (1994), species richness is a dynamic equilibrium of two opposing processes, namely disturbance (frequency or intensity) and rate of population growth and competitive displacement (i.e. productivity). Species richness is highest at particular combinations of disturbance and productivity, that is low disturbance/low productivity, intermediate disturbance/intermediate productivity, or high disturbance/high productivity. In low productivity ecosystems, growth is slow and competition is thus insufficient to result in species exclusion. In contrast, in productive ecosystems, without frequent disturbance, some species outgrow, dominate and competitively exclude other species, reducing species richness.

The structured manner in which data were collected in the FORESTCHECK project allows close examination of this theory. None of the species groups studied conformed with the theory. We recommend further analysis, however, with an expanded data set that includes a greater range of productivity types (e.g. karri forest, wandoo forest, riparian forest). Consistent with this result is a study of fire regime differences between sites in the southern jarrah forest. This found no significant difference in species richness (macrofungi, vascular flora, ants, beetles, frogs, reptiles and mammals) with variation in fire interval sequences (Wittkuhn *et al.* 2011).

Adequate nutrition is a fundamental requirement of life. In the impoverished soils of much of the jarrah forest, it is to be expected that abundance of species will be constrained by nutrients, particularly nitrogen (White 1993; Ricklefs 2008). Based on the research of Braithwaite (1983) and Braithwaite *et al.* (1983, 1984), differences between grids in soil nutrient concentrations

Table 4. Correlations of the abundance of species occurring on more than 40 sites with soil and foliar nutrients (tot = total, ex = extractable), disturbance due to silvicultural treatment (Dist. (log) = timber harvesting and associated fire), forest cover and basal area. Values followed by * are significant at $P < 0.05$; critical values are $r > 0.3$, $P < 0.05$; $r > 0.4$, $P < 0.01$, approximately.

Attribute	<i>Gerygone fusca</i> (bird)	<i>Acanthiza apicalis</i> (bird)	<i>Pardalotus striatus</i> (bird)	<i>Proteuxoa pissonephra</i> (moth)	<i>Agrotis munda</i> (moth)	<i>Ochrogaster lunifer</i> (moth)	<i>Hydrophilidae</i> sp. (14) (beetle)	<i>Tipulidae</i> sp. (16) (crane fly)	<i>Notodontidae</i> sp. (374) (moth)	<i>Galerina</i> sp. (macrofungus)	<i>Gymnopilus allantopus</i> (macrofungus)	<i>Gymnopilus</i> sp. slender (macrofungus)
Soil nutrients												
N	0.17	0.09	0.34*	0.13	0.30*	0.41*	0.46*	0.54*	-0.04	0.28	0.05	-0.26
P (tot)	0.40*	0.11	0.19	0.29*	0.37*	0.37*	0.44*	0.48*	0.19	0.24	0.10	-0.34*
P (ex)	0.36*	0.08	0.20	0.19	0.08	0.14	0.04	0.19	0.33*	0.28	0.03	-0.24
K (tot)	0.21	-0.10	0.01	0.61*	0.36*	0.10	0.65*	0.40*	-0.14	-0.11	-0.12	-0.29*
K (ex)	0.20	0.03	0.11	0.52*	0.48*	0.29*	0.66*	0.58*	-0.13	0.14	0.01	-0.25
Foliar nutrients												
Jarrah N	-0.06	-0.14	-0.01	-0.06	0.15	-0.03	-0.04	-0.02	0.03	-0.15	0.00	-0.02
Marri N	-0.21	-0.31*	0.09	0.20	0.09	-0.26	-0.02	0.12	-0.03	-0.21	-0.18	0.16
Jarrah P (tot)	0.02	0.06	-0.07	0.11	0.17	-0.17	0.05	0.04	-0.13	0.02	-0.20	-0.04
Marri P (tot)	-0.20	0.06	0.01	0.30*	0.21	-0.24	0.25	0.12	-0.38*	-0.17	-0.10	-0.05
Jarrah K (tot)	0.05	0.11	-0.11	0.07	0.27	-0.07	0.03	0.09	-0.10	0.00	-0.21	-0.03
Marri K (tot)	0.14	0.17	0.16	0.37*	0.17	0.05	0.44*	0.27	-0.10	0.08	0.22	-0.09
Other factors												
Forest cover	0.18	-0.29*	0.38*	-0.16	-0.16	-0.13	-0.10	-0.13	0.17	0.16	-0.02	-0.34*
Dist. (log)	-0.24	0.43*	-0.13	0.06	0.00	0.12	-0.07	-0.04	0.00	0.05	0.12	0.35*

were expected to contribute to variation in species richness and total abundance. However, FORESTCHECK revealed few instances of significant correlations (all positive) of species richness and total abundance with soil N, soil P or soil K, and the corresponding coefficients of determination were extremely low. Differences in foliar nutrients between jarrah and marri (Majer *et al.* 1992; Recher *et al.* 1996) were also expected to highlight the importance of marri in increasing the abundance of invertebrates present on foliage, and hence the increased abundance of insectivorous birds in grids with a greater proportion of marri present. Analyses in this study, however, revealed that this effect was weak.

The functional significance of singleton species may have several explanations (Main 1984). It may indicate the patchy occurrence of particular resources required by a species. For mobile species, it may indicate merely that singleton species occur at low density because of large home ranges. For sessile species, it may indicate the chance arrival of a fruit, seed or spore, occurrence within a seral stage unfavourable to the species, or a relictual distribution following population reduction within the geographical range of the species. Singleton species may also provide greater resilience to an ecosystem by acting as insurance policies in case of disruption to ecosystem processes (Main 1981; Walker *et al.* 1999). For example, with climate change some singleton species could become dominant species and mitigate any alteration to ecosystem processes.

This overview has not attempted a functional study to complement the taxon-based studies of Abbott *et al.* (2011), Cranfield *et al.* (2011), Farr *et al.* (2011), McCaw (2011), Robinson and Williams (2011), Ward *et al.* (2011) and Wayne *et al.* (2011). For the purpose

of this synthesis, it proved difficult to define functional groups so that they are neither too broad nor too narrow, as well as to assign species to functional groups. 'Herbivore' or first-order consumer is too broad to include very different ways of living in an ecosystem, for example folivorous animals, seed-eating birds and insects, nectar-feeding birds, and wood-degrading termites and fungi. Furthermore, many species are omnivores, eating fruits and insects, or eating fungi, insects and small vertebrates. Once these issues are resolved, the FORESTCHECK dataset certainly offers considerable potential for further analysis.

Comparison of biodiversity monitoring and bio-indicator monitoring

Many studies have addressed the need to monitor the consequences of human activity in ecosystems, not just for the purpose of documenting or quantifying negative impacts but to assess which activities minimise environmental harm. There is consensus that every entity and process cannot be monitored. Opinion is divided as to the best focus, including use of headline indicators that integrate many components, species known to be sensitive to environmental change, significant species, or whether a composite set of complementary indicators is necessary (Noss 1990; Lawton *et al.* 1998; McLaren *et al.* 1998).

The bio-indicator approach was deliberately avoided in the FORESTCHECK program, for several reasons (Abbott and Burrows 2004): First, it was considered high risk to identify suitable taxa given the inadequate state of knowledge of fungal and invertebrate species and their distribution in forests; second, the public needs re-assurance that controversial activities such as timber harvesting

are not causing local extinctions of any species; and finally, the biodiversity approach is more precautionary than the bio-indicator approach in that it allows subsequent selection of indicators from a better informed and more confident basis. Failing and Gregory (2003) have suggested that direct answers to the questions *Is this ecosystem 'healthy'?* and *Is this ecosystem recovering from disturbance?* are required, rather than lists of indicators. Species richness and total abundance are two of the most fundamental indicators. Because most species in an ecosystem are naturally rare (e.g. Hubbell 2001), a biodiversity approach rather than a bio-indicator approach is appropriate.

The premise of bio-indicator monitoring is that each of the selected bio-indicator species is sufficiently well studied that it is highly certain that its abundance constitutes a measure of how well its ecological requirements are satisfied at a particular location. These species, sometimes called focal, umbrella, flagship or surrogate species, are usually common but vulnerable to known threatening processes (Caro and O'Doherty 1999). Application of this to forests seems simple—bio-indicators can be selected from well-studied groups (usually birds and mammals) or from species that require particular resources likely to be sensitive to timber harvesting, such as the density of nest hollows in standing trees and the density of understorey. However, the assumption that the few species monitored provide a reliable guide to all other species not studied is questionable (D'Eon *et al.* 2004). Andelman and Fagan (2000) demonstrated that surrogates performed no better than a comparable set of species randomly selected from a database. Selected indicator species may or may not be appropriate. For example, Suter *et al.* (2002) found that a species of grouse was a poor indicator of bird diversity in Switzerland, whereas woodpeckers were a useful indicator of forest bird diversity in Poland (Mikusiński *et al.* 2001). Forests in Italy occupied by raptors had more species of birds, butterflies, and trees present (Sergio *et al.* 2006). The FORESTCHECK study showed that very few species were sufficiently widespread to be potentially useful as bio-indicators (prevalence greater than 80%), and only three bird species and no terrestrial vertebrate species qualified. Additionally, these species were more likely to increase in abundance in response to disturbance.

The obvious shortcoming of indicator species is that they do not provide any information about declines, extinctions or increases of species that are not monitored. An unfortunate by-product of the indicator approach is that it results in data able to be collected at little extra cost or time being neglected. When trapping small mammals and reptiles, counting birds, or noting the occurrences of plant species, why should information on non-indicator species not be recorded? The danger with the indicator approach is that it can turn short cuts necessitated by shortage of funds, time or other resources, as well as reasons of convenience, into a false virtue.

As data accrue, however, it should be possible to make a more confident selection of species that range widely in jarrah forest, have known response and sensitivity to timber harvesting, are easily sampled, and are not confusable with other species. As additional sites are sampled over the same large spatial scale, more species should accumulate from the reference grids. Localised (within-ecosystem) comparisons found no differences in observed richness between treatments, while there was greater estimated richness in reference grids at the bioregional scale.

Implications for forest policy, practice and research

No urgent corrective actions appear necessary at this stage, given the extensive area of forest now reserved from timber harvesting: no species were found to be the equivalent of 'the canary in the coalmine'. Attention, however, needs to be given to determining why regeneration stocking did not attain the specified standard in some grids. The species group most sensitive to silvicultural disturbance, cryptogams (particularly lichens), merits detailed research into the population ecology of these species in order to determine the exact mechanism of the detrimental silvicultural impact. Because no abundance data were collected for cryptogams, it is not possible to identify which species were most affected. Further investigation of why more singleton species of vascular flora and cryptogams were recorded in reference grids than disturbed grids is also required.

Unforeseen benefits of FORESTCHECK monitoring

Although the focus of FORESTCHECK is the impacts of silvicultural disturbance on biodiversity, regeneration and soils, the results also provide a sound basis for a systematic biological survey of the forest. As the extent of timber harvesting in native forest continues to decline, following a shift in societal values since the 1990s, FORESTCHECK can contribute to improved knowledge of the ecology of these forests. The scope and breadth of the project could be expanded to encompass sites within and adjacent to jarrah forest that are not dominated by jarrah trees. Examples include forest dominated by karri (*Eucalyptus diversicolor*) or wandoo (*E. wandoo*), lithic complex (heath), riparian habitat (heath with *E. rudis*, *E. megacarpa* or *E. patens*), *Banksia* woodland and kwongan (heath). Catenary sequences, from stream edge to ridge top, in both highly dissected and subdued terrain should also be included. This approach would detect both local and regional species richness patterning and gradients, and would enable further adjustment of the forest conservation estate as well as improved forest management.

FORESTCHECK has the potential to provide a superior model for systematic biological survey. Conventional biological surveys invariably select minimally disturbed areas of native vegetation (e.g. Keighery 2004) and avoid areas disturbed by fire, grazing or cropping. In doing so, this approach overlooks the role of disturbance in shaping biodiversity (e.g. Huston 1994), the contribution of off-reserve tenures (such as state forest) to nature conservation (Shea *et al.* 1997), and the vital clues supplied to land managers in providing a balanced mosaic of disturbance across the landscape.

FORESTCHECK could also be used to monitor the impacts of planned fires (prescribed burning) and climate change on regeneration, soil and biodiversity attributes of forests (Burrows and Abbott 2003; Abbott and LeMaitre 2010).

Data collected from the 19 grids that had either never been harvested or not harvested for timber for four decades deserve further analysis. This could include the effect of time since the last fire, basal area, soil and foliar nutrients etc. on species richness and total abundance, as well as on the abundance of species of particular interest, without the confounding effect of harvesting.

Implications for improved monitoring and analysis: what could have been done better?

Substantial effort was put into selecting, locating, checking and demarcating the 48 grids that comprise phase 1 of the FORESTCHECK monitoring program (McCaw *et al.* 2011). Although a broad array of forest and biodiversity factors have been sampled, the grids could be sampled for many other factors. The opportunity for doing so, however, is receding as planned fire will be imposed on all grids within the next ten years. It is highly desirable, for example, that groups such as nematodes, soil micro-organisms (including bacteria and mycorrhizal fungi) and bats are studied. Such investigations are limited only by the expertise and interest within academia, the availability of honours and doctoral students, and by financial resources.

The second recommendation is that the condition of the landscape surrounding each grid be quantified. The proportion of forest never harvested for timber, forest not recently harvested for timber, forest recently burnt (by wildfire or by planned fire) and forest cleared for farming within 500-m, 1-km, 2-km and 5-km radii would permit evaluation of the influence of the broader landscape on ecological processes and species richness and composition.

The final recommended improvement is the integration of the results of FORESTCHECK with numerous other site-based studies in south-west WA that have used or are using sampling protocols identical or similar to FORESTCHECK. The oldest of these is the Kingston study (Burrows *et al.* 1993), which was a short- to intermediate-term (1994–2001) longitudinal study of silvicultural impacts on vascular flora, invertebrates, birds and mammals (Burrows *et al.* 2001; Morris *et al.* 2001; Abbott *et al.* 2003a,b; Craig and Roberts 2005). It was based on a BACI (before–after, control–impact) experimental approach, but did not include cryptogams or macrofungi. The Walpole Fire Mosaic study, which commenced in 2004, is comparing the impact on all biodiversity groups sampled by FORESTCHECK of fine-scale habitat heterogeneity produced by frequent, low-intensity fire with habitat homogeneity resulting from infrequent, higher-intensity fire (Burrows *et al.* 2004). Another study of the impact of fire regime (the number of fires in a defined period), rather than the effect of the period since the last fire, was recently completed (Pekin *et al.* 2009; Wittkuhn *et al.* 2011). In this study only vascular flora, macrofungi, some invertebrates and some vertebrates were sampled.

The Kingston, Walpole Fire Mosaic, and Fire Regime studies differ in their spatial and temporal scales. The outcome from integrating and synthesising the results of these complementary studies with those from FORESTCHECK should provide a more holistic understanding of forest ecology in south-west WA.

Limitations of the FORESTCHECK study

Because each forest ecosystem was studied in a different year, year of study and forest ecosystem type are confounded. This resulted from the major purpose of the program—to study silvicultural impacts on ecological process and species groups. It was not feasible with the available resources to sample all 48 grids in the one year. However, in phase 2 of the FORESTCHECK project (2008–2012), all of the grids sampled during phase 1 (2001–2006) are being revisited. The results will resolve the relative importance of year of sampling *cf.* forest ecosystem.

The principal limitation is the retrospective focus of FORESTCHECK, in which space is substituted for time (chronosequence). It can never be ascertained that within a forest ecosystem the principal difference between grids is in the silvicultural treatment imposed, despite considerable effort in minimising variation in soil type, vegetation type, average annual rainfall, elevation, slope and aspect between grids (McCaw *et al.* 2011). However, this is addressed through spatial and temporal replication. Comparison with longitudinal studies, such as the Kingston study, will reveal if this is a major limitation. Although longitudinal studies are more rigorous than retrospective studies, their main disadvantage is that they require many years of regular monitoring. This entails a risk that the biodiversity of large areas of forest subject to a particular method of timber harvesting may have been compromised before this is revealed by a longitudinal study. Longitudinal studies also require the long-term investment of resources that may not continue to be made available.

Although monitoring is methodical, it is neither scientific research nor a substitute for it (Burrows and Christensen 2002). Monitoring demonstrates long-term trends in the performance of measured attributes. Trends that show decline or decrease, or slow increase, alert forest managers to the need to investigate further, and this will usually entail specific experiment-based research. Cryptogams, as well as those species listed in Table 4 that correlate negatively with forest cover or with timber harvesting and associated fire, would be prime candidates for such study.

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