

# In defence of small habitat islands: Termites (Isoptera) in the Western Australian central wheatbelt, and the importance of dispersal power in species occurrence

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Ecological theory has long undervalued the contribution of small remnants of native vegetation to nature conservation. This study provides data on colony persistence of remnant-dependent wood-eating termites in 28 remnants of mature wandoo (*Eucalyptus capillosa*) trees in paddock situations in the agricultural south-west of Western Australia. Remnants ranged in size from 2 to 30 trees, and in spatial isolation from 50 to 650 m. All remnants have been exposed to livestock-related disturbance for >40 years.

This study found that: (1) Small remnants of eucalypt trees on farms retain important functional representatives, i.e., wood-eating termites for nutrient-cycling, and high species numbers. (2) Seventeen species have the capacity to establish and maintain colonies in remnants  $\leq 5$  trees. (3) Spatial isolation has no significant influence on the total number of termite species. (4) The number of trees ( $r = 0.60$ ) and quantity of dead wood in the remnant ( $r = 0.86$ ) were significant indicators of total termite species number. Larger remnants with low quantities of wood supported few termites, however. (5) Rare as well as common species persisted in small remnants. (6) Alate wing-size was a significant indicator of the occurrence of the six most common termite species in remnants ( $r = 0.84$ ).

The implication of isolation effects for rare species with limited powers of dispersal is self-evident, as is the need for the creation of habitat linkages to reduce the effects of spatial isolation on the native fauna.

Key words: Dispersal power, Fragmentation, *Eucalyptus* remnants, Termites.

## INTRODUCTION

ISLAND biogeography theory (MacArthur and Wilson 1967) served as an approach to tackle conservation issues in fragmented (agricultural) landscapes. The theory focused on species number in relation to area (community-oriented), but paid little attention to species identity (population-oriented). Yet, species often differ in their ability to cope with human-induced changes in the environment and communities in fragmented ecosystems may consist largely of disturbance opportunists of low conservation value. A consequence of the theory's emphasis on species number is that it effectively devalued small habitat islands for nature conservation (Simberloff 1997), as did the 50/500 rule of genetics, which refers to the population size needed to preserve genetic variance (Frankel and Soulé 1981). Whereas the relationship between island size and species number remains relevant for nature conservation, population persistence in fragmented landscapes has become the major focus of research and management (Simberloff 1997).

Metapopulation theory has now largely replaced island biogeography theory as a framework for the conservation of fragmented populations and has given new significance to small habitat islands (Hanski and Simberloff 1997). The significance of metapopulation theory is that, given that a distance between islands is within

the dispersal capability of species (e.g., flight distance), inter-island recruitment can provide temporary relief from local extinction. The exchange of only a few individuals between local populations can reduce population size fluctuations and so decrease the risk of extinction (den Boer 1990). Populations on small islands are thus valuable resources and, wherever possible, should be maintained. However, with few exceptions (e.g., Majer and Delabie, in press), data on species persistence in very small habitat islands are scarce.

The central wheatbelt of Western Australia provides a good example of where clearing and associated habitat fragmentation has caused massive declines in population sizes (e.g., Smith 1998), reducing most of the native biota to persist in remnants of varying size, spatial isolation, habitat composition and degree of degradation (Hobbs 1987; Arnold and Weeldenburg 1991; Saunders *et al.* 1991; Abensperg-Traun *et al.* 1996a). The present study builds on three previous investigations of the persistence of terrestrial arthropods in small remnants in the study area (Abensperg-Traun *et al.* 1996a; Abensperg-Traun and Smith, in press; Majer *et al.*, in press), and records the presence of wood-eating termite colonies in remnants of wandoo woodland. Factors potentially influencing persistence of termite colonies that were investigated are

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(i) number of eucalypt trees (remnant size), (ii) distance to the nearest potential source of colonizers (spatial isolation), (iii) quantity of dead/decaying wood (availability of food and nest sites), and (iv) alate wing-size (termite dispersal power) for individual species.

### Why termites?

In arid and semi-arid regions of Australia, termite biomass, together with that of the ants, has been estimated to far exceed the combined biomass of native and non-native mammalian herbivores (Watson *et al.* 1973), and this reflects their pivotal ecological role in these regions (Abensperg-Traun 1994; Lobry de Bruyn and Conacher 1995). Their persistence in remnant vegetation is thus of considerable functional importance, such as for eucalypt woodlands in the study area where termite abundance can be especially high (Abensperg-Traun and De Boer 1990).

Clearing of native vegetation, and prolonged cultivation, results in the complete destruction of termite communities (Holt *et al.* 1993). Some 40+ years after clearing and cultivation, wood-eating termites are restricted to habitat islands within the adjacent agricultural matrix, making them an appropriate target for this investigation. Wood-eaters are readily located where they forage (dead/decaying wood), so it is relatively easy to census their presence in remnants.

All termites disperse predominantly by air but different termite species appear to differ in dispersal power (Nutting 1969). The dispersing "units" are winged male or female reproductives, referred to as "alates". Differential dispersal power has important implications for persistence in fragmented landscapes (Den Boer 1990). One important (measurable) factor influencing dispersal power is likely to be the size of the forewings. The importance of alate wing-size in termite dispersal has never been quantified.

## METHODS

### Study area and study remnants

The environmental background (climate, soils) and plant floristics of wandoo *Eucalyptus capillosa* woodland have been described by Beard (1980) and McArthur (1991, 1993).

A "remnant" is defined as a stand of wandoo trees, of varying size (number of trees) and isolated from other remnants by an agricultural matrix consisting of annual crops such as wheat or lupin, or pasture. Crops are rotated with pasture at 2 to 3-year intervals, so the matrix surrounding remnants varies frequently. Twenty-eight remnants of wandoo trees were selected for study, using a range in sizes and degrees of spatial isolation as selection criteria.

Table 1. Summary statistics for remnant characteristics and numbers of termite species for remnant stands of wandoo *Eucalyptus capillosa* trees. \* = subjective score: 1 = low quantity; 2 = moderate quantity; 3 = high quantity; 4 = very high quantity (see Methods for detail).

Variable	Mean ± S.D.	Range
No. trees in remnant	10.6 ± 8.6	2–30
Distance (meters) to the nearest potential source of colonizers	212 ± 174	50–650
Quantity of dead/decaying wood in remnant*	2.39 ± 1.25	1–4
No. wood-eating termite species	5.25 ± 3.40	1–11

Remnants ranged in size from 2 to 30 trees and in spatial isolation from 50 to 680 m (Table 1). All remnants had been exposed to livestock-grazing/trampling and fragmentation effects (e.g., weed invasion, soil compaction, increased insolation) for at least 40 years and had lost all their native shrubs and most or all of their annual grasses and herbs (e.g., Abensperg-Traun *et al.* 1998). All study remnants were unfenced and were distributed across a 40 × 40 km study area north of the wheat-belt town of Kellerberrin (~31°25'S, 117°26'E) which has been described in detail elsewhere (Saunders *et al.* 1993; Abensperg-Traun *et al.* 1996a,b).

### Data collection and analysis

The total number of trees was counted for each remnant, and its distance in meters from the edge of the remnant to the nearest source of potential colonizers (i.e., road-verge vegetation, larger remnant) was measured. Remnant stands of wandoo trees were sampled once, in spring (September 1998) when the combination of soil moisture and temperature guaranteed optimal termite activity levels and hence sampling conditions (Abensperg-Traun and De Boer 1990; Abensperg-Traun 1991). All dead/decaying wood lying on the ground was turned over and carefully examined for termites, and soldiers were collected for species identification using the author's reference collection for the study area. This method excludes termite species feeding on roots of standing dead trees because of the destructive nature of this sampling method, and thus underestimates species number in remnants.

The relationship between termite species number with both the number of trees in the remnant, and their degree of spatial isolation was examined using simple linear regression analysis on untransformed values, assuming that total termite species number is partially a function of remnant size (numbers of trees) and

spatial isolation. Woodland remnants were also examined for their suitability to support wood-eating termites. Quantity (approximate length in meters) of dead/decaying wood (>5 cm in diameter) lying on the ground, as an indicator of food and nest site availability, was subjectively ranked: 1 = <5 m (low quantity, 10 remnants); 2 = 5 to 10 m (moderate quantity, 5 remnants); 3 = 11 to 20 m (high quantity, 5 remnants); 4 = >20 m (very high quantity, 8 remnants). Spearman rank correlation was used to examine the relationship between ranked numbers of termite species and the ranked quantity of dead wood on the ground. Termite species number ranks were: 1 = <3 spp. (6 remnants), 2 = 3 to 6 spp. (11 remnants), 3 = 7 to 9 spp. (6 remnants), and 4 = >9 spp. (5 remnants).

Analysis of the relationship between alate wing-size and termite species occurrence in remnants was restricted to seven species that occurred in eight or more (35%) of study remnants. First, because of analytical rigour (sample size), and second, because data on

alate wing-length for the majority of other species are not available. Data on forewing-length for respective species was taken from Hill (1942), using median values of specimens collected in Western Australia. Simple linear regression on untransformed data was used to examine the relationship between species occurrence and wing-size.

**RESULTS**

Summary statistics for remnant characteristics and termite species numbers are given in Table 1. A total of 29 termite species from two families and 14 genera were identified, and numbers of species for individual study remnants ranged from one to 11 species. The genus *Amitermes* was the richest in species (11 spp.). One species of *Tumulitermes* (*T. sp. nov.*), not previously recorded for the region, was located in a 20-tree remnant with abundant dead wood on the ground, and isolated by 160 m from road-verge vegetation. Table 2 summarizes observations on the occurrence for individual termite species. Twenty-two species

Table 2. Summary statistics for the occurrence of wood-eating termite species (Isoptera) in remnant stands of mature wandoo *Eucalyptus capillosa* trees. \* = as a measure of the availability of surface food and nest sites: 1 = low quantity; 2 = moderate quantity; 3 = high quantity; 4 = very high quantity (see Methods for detail). \*\* = species used in analysis of relationship between alate wing-size and species occurrence.

Species	No. remnants where species recorded	Smallest remnant (No. trees) where present	Distance (m) to nearest source at smallest remnant	Greatest distance (m) to nearest source	Lowest category of dead/decaying wood in remnant*
<b>Rhinotermitidae</b>					
<i>Copiotermes acinaciformis</i> **	16	2	50	650	1
<i>Heterotermes occiduus</i> **	9	2	60	440	1
<i>Heterotermes paradoxus intermedius</i> **	9	2	50	650	2
<i>Schedorhinotermes reticulatus</i> **	11	2	60	650	1
<b>Termitidae</b>					
<i>Amitermes calabyi</i>	5	3	50	320	2
<i>Amitermes dentosus</i>	3	3	150	210	3
<i>Amitermes hartmeyeri</i>	3	5	120	410	4
<i>Amitermes neogermanus</i> **	11	2	60	440	1
<i>Amitermes obeuntis</i> **	17	2	50	440	1
<i>Amitermes perarmatus</i>	1	18	340	340	3
<i>Amitermes procerus</i>	1	5	650	650	1
<i>Amitermes sp. 1</i>	6	5	120	440	4
<i>Amitermes sp. 2</i>	3	18	340	340	3
<i>Amitermes sp. 3</i>	1	3	150	150	2
<i>Amitermes sp. 4</i>	2	4	90	90	4
<i>Ekphysotermes kalgoorliensis</i>	1	22	50	50	4
<i>Ephelotermes argutus</i>	4	9	140	180	1
<i>Ephelotermes persimilis</i>	2	21	120	180	3
<i>Microcerotermes distinctus</i>	5	2	160	650	1
<i>Microcerotermes newmani</i> **	8	2	50	650	1
<i>Nasutitermes exitiosus</i>	4	5	120	440	1
<i>Occasitermes occasus</i>	3	9	140	440	4
<i>Paracapritermes kraepelinii</i>	5	2	60	650	1
<i>Termes-Capritermes complex sp. 1</i>	1	20	440	440	4
<i>Termes-Capritermes complex sp. 2</i>	1	21	340	340	3
<i>Tumulitermes peracutus</i>	3	5	120	410	4
<i>Tumulitermes petilus</i>	6	3	150	650	2
<i>Tumulitermes sp. nov.</i>	1	20	160	160	4
<i>Xylochomitermes occidualis</i>	4	19	90	410	4

(76% of total species) were recorded in <8 remnants. The most common species (present in  $\geq 8$  remnants) were: Rhinotermitidae, *Coptotermes acinaciformis*, *Heterotermes occiduus*, *H. paradoxus intermedius*, *Schedorhinotermes reticulatus*; Termitidae, *Amitermes neogermanus*, *A. obeuntis* and *Microcerotermes newmani*.

#### Number of trees and quantity of dead/decaying wood in remnants

The number of eucalypt trees in remnants was a significant indicator of the number of termite species ( $r^2 = 0.42$ , Fig. 1). Three remnants with 17 or more trees shared the highest number of termite species (11 spp.). Smaller remnants also supported a surprisingly high number of species: e.g., four spp. for two trees, six spp. for three trees, 10 spp. for five trees. The largest remnant did not support the highest number

of termite species, and two moderately-sized remnants (of 14 and 17 trees, respectively) each supported a single species only (Fig. 1). Both of these latter remnants contained low quantities of dead wood. The relationship between number of trees and quantity of dead wood was statistically significant ( $r = 0.70$ ,  $P = 0.01$ ).

Figure 2 shows the cumulative number of termite species that have demonstrated their ability to establish and maintain colonies in very small remnants. An example is 17 species that, individually, were located in remnants comprising  $\leq 5$  trees.

The ranked quantity of dead/decaying wood was a significant indicator of (ranked) termite species number ( $r^2 = 0.75$ , Fig. 3), although wood categories one and two supported similar numbers of termite species.

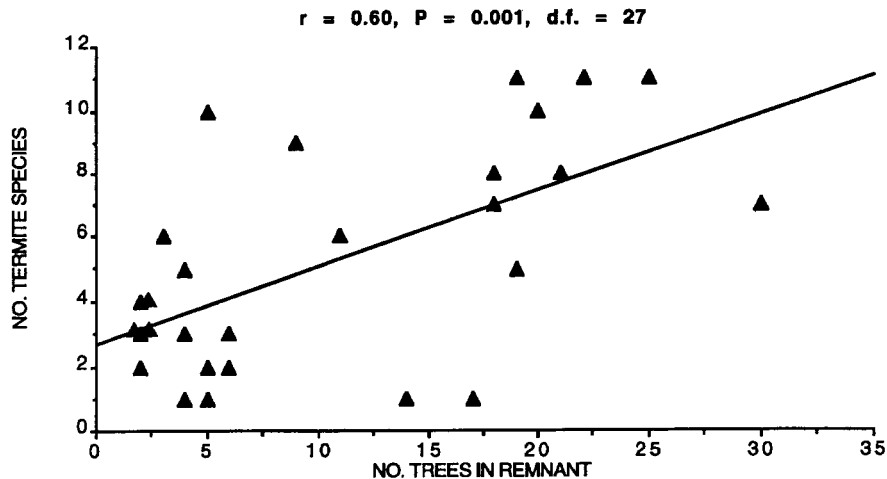


Fig. 1. Relationship between the number of wandoo (*Eucalyptus capillosa*) trees in study remnants, and the number of wood-eating termite species.

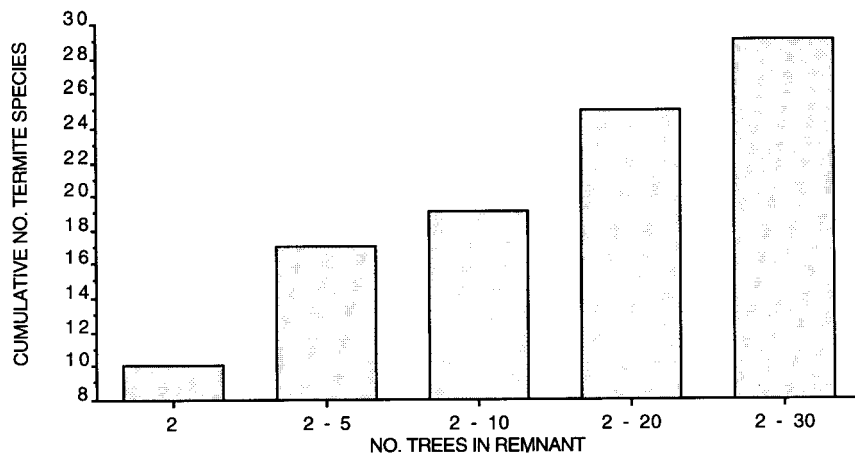


Fig. 2. The cumulative number of wood-eating termite species that have shown their ability to establish and maintain colonies in remnants of different size categories (number of wandoo *Eucalyptus capillosa* trees).

**Remnant isolation and termite dispersal power**

Remnant isolation had no significant influence on the total number of termite species ( $P = >0.05$ ).

Based on the seven most common termite species, however, alate wing-size of respective species was positively associated with species occurrence in remnants (Fig. 4). Species with large-winged alates were more commonly encountered in remnants than species with

smaller-winged alates. Due to the small sample size, the relationship was not statistically significant, however ( $r^2 = 0.36, P = >0.05$ ).

*Coptotermes acinaciformis* was recorded for a markedly higher number of study remnants (16 remnants), despite the relatively small wing-sizes of its alates. When the ubiquitous *C. acinaciformis* was excluded from the analysis, the percentage variation in species occurrence explained by wing-size increased to 70% (Fig. 4).

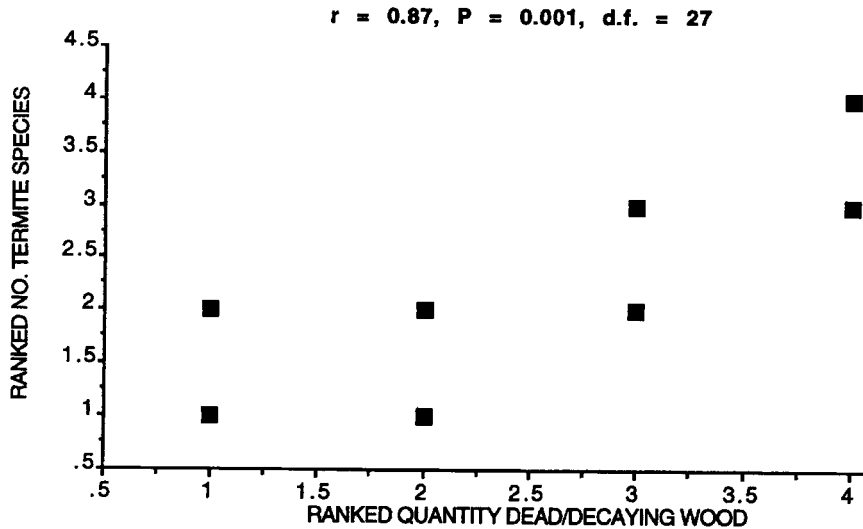


Fig. 3. Relationship between the ranked quantity of dead/decaying wood in remnants, and the ranked number of wood-eating termite species. Ranked quantities of dead/decaying wood are: 1 = low quantity (10 remnants); 2 = moderate quantity (5 remnants); 3 = high quantity (5 remnants); 4 = very high quantity (8 remnants) (see Methods for further details). Termite species number ranks were: 1 = <3 spp. (6 remnants), 2 = 3 to 6 spp. (11 remnants), 3 = 7 to 9 spp. (6 remnants), and 4 = >9 spp. (5 remnants).

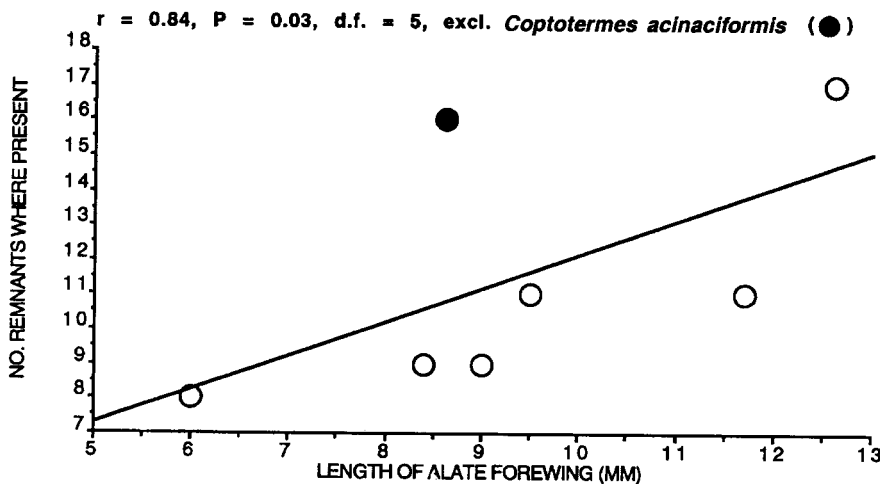


Fig. 4. Relationship between length of the forewing (mm) of alates (male/female reproductives) of the seven most common wood-eating termite species (present in  $\geq 8$  study sites), and the number of remnant stands of wandoo *Eucalyptus capillosa* trees from which respective species were recorded. Termite species used in the analysis were: Rhinotermitidae, *Coptotermes acinaciformis* (length of forewing 8.6 mm, shown as solid point), *Heterotermes occiduus* (9 mm), *H. paradoxus intermedius* (8.4 mm), *Schedorhinotermes reticulatus* (9.5 mm); Termitidae, *Amitermes neogermanus* (11.7 mm), *A. obeuntis* (12.6 mm), *Microcerotermes newmani* (6 mm).

Similarly, when the occurrence of the six most common species (*C. acinaciformis* excluded) was then regressed against remnants of progressively increasing levels of spatial isolation, the furthest distance category (greatest isolation) showed the highest, and statistically significant, regression coefficient between wing-size and species occurrence (Table 3).

Table 3. Relationships (simple linear regressions) between the occurrence (numbers of remnants where present) of the six most common termite species (excluding the ubiquitous *Coptotermes acinaciformis*, see text) and alate wing-size of respective termite species for groups of remnants of different degrees of spatial isolation (distance to the nearest potential source of colonizers). Five degrees of freedom for all categories of spatial isolation.

Distance to nearest source	Total No. remnants	r	r <sup>2</sup>	p
≥50 m	23	0.78	0.61	0.06
≥100 m	20	0.78	0.61	0.06
≥150 m	13	0.76	0.58	0.08
≥200 m	10	0.90	0.81	0.01

## DISCUSSION

The major findings of this study are summarized as follows: (1) Small remnants of eucalypt trees on farms retain important functional representatives, i.e., wood-eating termites for nutrient-cycling, and surprisingly high species numbers. (2) Individually, a high number of termite species have demonstrated their ability to establish and maintain colonies in very small remnants. (3) Distance to a potential source of colonizers had no significant influence on the total number of termite species. (4) Number of trees, and quantity of dead wood, were significant indicators of the number of termite species in remnants. Larger remnants with low quantities of dead wood supported few species, however. (5) Common as well as rare species persisted in small groups of eucalypt trees. (6) The occurrence of the six most common termite species was strongly associated with alate wing-size.

A decline in termite species number with remnant size partially supports island biogeography theory and is consistent with other studies on termites in small habitat fragments (De Souza and Brown 1994 for Amazonian forest fragments; Abensperg-Traun *et al.* 1996a for the study area). However, remnant "quality" also influenced species numbers. In addition to dispersal power, colony longevity is likely to be a critical factor contributing to species persistence in remnants. Whereas colony longevity could not be measured, there are reasons to suggest that it is likely to have declined following the fragmentation period.

## Colony longevity

The maximum lifespan of most termite colonies is about 20 to 25 years (Wood and Johnson 1986) and few, if any, colonies alive at the time of the fragmentation event (40 years +) are likely to have survived to this day. Colony longevity is, in part, related to colony vigour (e.g., reproductive output, susceptibility to predation; Wood and Johnson 1986). Indirect evidence for a decline in termite colony vigour in small remnants in the study area comes from two sources. First, mound heights in small remnants are lower, and rates of mound abandonment are higher, relative to mounds in large, relatively undisturbed woodlands (Abensperg-Traun and Smith, in press). Second, there has been a marked reduction in termite abundance and diversity in small, livestock-grazed gimlet *Eucalyptus salubris* woodland (Abensperg-Traun *et al.* 1996a).

## Dispersal power

The presence of colonies in study remnants may be attributed in part to colonization from other remnants, and to *in situ* (within-remnant) dispersal. Alates with large wings should be able to fly further than small-winged alates, thus favouring them to reach remnant islands some distance away. The positive relationship between alate wing-size and species occurrence implies that: (i) alate wing-size may be an effective indicator of dispersal power in termites, and that, depending on degree of isolation, inter-remnant recruitment may be largely restricted to species with large-winged alates; (ii) species recruitment via intra-island dispersal may play an insignificant role in small remnants; and (iii) colony death in habitat islands may be a common event. Inter-remnant recruitment may thus be an important factor in providing temporary relief from local extinction. The extent to which termite colonies in these woodland remnants function in a metapopulation sense (Simberloff 1997) remains to be established, however. The precise mechanisms resulting in local extinctions remain unknown, but predation by aggressive predaceous ants of the *Iridomyrmex rufoniger* group, for example, are likely contributors to colony death in highly disturbed circumstances (Abensperg-Traun *et al.* 1996c).

Higher than expected occurrence (based on alate wing-size) of *Coptotermes acinaciformis* demonstrates that the factors contributing to population persistence can not be explained by alate wing-size alone. There are three plausible explanations for the greater persistence of *C. acinaciformis*, relative to other common species with comparable (small) wing-sizes. First, large colonies tend to live longer than small colonies (Wood and Johnson 1985), hence

species with large colonies are more likely to persist in small remnants than species with small colonies. Together with *Nasutitermes exitiosus*, colonies of *C. acinaciformis* are by far the largest among the termite fauna in the study area, and single colonies can consist of well in excess of a million individuals (Greaves 1967; Gay and Wetherley 1970). Colony longevity also depends upon the species' ability to replace lost primary reproductives (e.g., loss of queen following predation, or death due to old age). Replacement of lost reproductives is known to occur in some Australian species of *Coptotermes* (Lenz and Barrett 1982), but is poorly known for the great majority of species (Watson and Gay 1991). The presence of long-lived species may mask isolation and disturbance effects.

Second, species with large colonies are likely to produce much higher numbers of alates per season than species with small colonies (Brian 1978), and this should facilitate comparatively high rates of remnant recolonization.

Third, competition between termite colonies is poorly known but has been demonstrated for some eastern Australian species (Wood and Lee 1971). Inter- and intra-specific competition for food and nest sites in small remnants is likely to be intense, and large colonies of *C. acinaciformis* may be more effective in securing the necessary resources for persistence, with small colonies experiencing increased stress, and possibly higher rates of predation (Abensperg-Traun *et al.* 1996c).

Low occurrence of the large colonies of *Nasutitermes exitiosus* in remnants, despite the large wing-size of the species' alates (~14.5 mm, Hill 1942), and its common status in less disturbed wandoo woodland in the study area, is likely to be due to the species' soft earth mounds which must be highly susceptible to prolonged sheep-trampling. The two other mound-building wood-eaters in study remnants (*C. acinaciformis*, *Amietermes obeuntis*) construct very hard clay mounds of low susceptibility to hoof damage. Both of the latter species are common in small remnants (this study; Abensperg-Traun and Smith, in press for *A. obeuntis*).

The implication of the above findings on likely isolation effects for rare species with limited powers of dispersal is self-evident. Differential persistence related to dispersal power provides a strong argument in favour of the creation of habitat linkages (corridors).

#### Other considerations

Retention of faunal components for different ecological functions (e.g., nutrient-cycling, predation) is just as important in small on-farm vegetation remnants as it is in larger protected areas such as reserves. This is particularly the

case in places such as the study area, where remnant elements of the original landscape will provide the building blocks for future ecosystem restoration which has been canvassed elsewhere (Main 1987; Hobbs and Saunders 1991; Lefroy *et al.* 1993). Given that individual farmers and landcare groups in the study area have demonstrated great enthusiasm to revegetate strategic parts of their farms, remnant groups of eucalypt trees should be integrated with such revegetated areas, particularly those aimed at reducing soil salinity, which are the majority. But trees alone are inadequate to sustain a wide range of wood-eating termite species because variation in habitat suitability also influenced species persistence in the study remnants. The importance of the availability of appropriate food and nest sites to attract and subsequently sustain species has been shown for other terrestrial arthropods elsewhere in south-west Western Australia (e.g., Majer and Nichols 1998 for ants).

The answer to the question of whether small remnant groups of eucalypt trees matter, is an emphatic *yes*. But, this is an idealist's view of the world. Clearly, the biological integrity of remnants of such size, and even those considerably larger, is continuously compromised by a multitude of factors originating from inside and from outside remnants (e.g., Hobbs 1987; George *et al.* 1995; Abensperg-Traun *et al.* 1996a, 1998). Few remnant eucalypt woodlands in the study area, irrespective of size, are likely to be self-sustaining, particularly in the absence of fire and in the presence of sheep, cattle or rabbits, and weed invasion (Burrows *et al.* 1990; Wilson 1990; Abensperg-Traun *et al.* 1998), although grazing effects, and associated levels of weed invasion, differ for different types of eucalypt woodland (Abensperg-Traun *et al.* 1998, in press). Also, funds aimed at preserving native plants and animals are far below what are needed, and nature conservation may have to ride "piggy-back" with revegetation projects aimed at soil conservation (Hobbs 1993). The hope is that species can persist until landscape restoration will start to make a difference for native plants and animals. The scale of the problem is daunting, however. It is highly probable that more species will be lost until the time when ecosystem restoration starts to take effect at a scale that goes beyond the individual farm. Until then, we need to remember that while large is clearly beautiful, large *and* small habitat islands contribute to sustaining the native biota in the short to medium term.

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## REFERENCES

- Abensperg-Traun, M., 1991. Seasonal changes in activity of subterranean termite species (Isoptera) in Western Australian wheatbelt habitats. *Aust. J. Ecol.* **16**: 331–36.
- Abensperg-Traun, M., 1994. The influence of climate on patterns of termite-eating in Australian mammals and lizards. *Aust. J. Ecol.* **19**: 65–71.
- Abensperg-Traun, M. and De Boer, E. S., 1990. Species abundance and habitat differences in biomass of subterranean termites (Isoptera) in the wheatbelt of Western Australia. *Aust. J. Ecol.* **15**: 219–26.
- Abensperg-Traun, M., Smith, G. T., Arnold, G. W. and Steven, D. E., 1996a. The effects of habitat fragmentation and livestock-grazing on animal communities in remnants of gimlet *Eucalyptus salubris* woodland in the Western Australian wheatbelt. I. Arthropods. *J. Appl. Ecol.* **33**: 1281–301.
- Abensperg-Traun, M., Arnold, G. W., Steven, D. E., Smith, G. T., Atkins, L., Viveen, J. J. and Gutter, M., 1996b. Biodiversity indicators in semi-arid, agricultural Western Australia. *Pac. Cons. Biol.* **2**: 375–89.
- Abensperg-Traun, M., Steven, D. E. and Atkins, L., 1996c. The influence of plant diversity on the resilience of harvester termites to fire. *Pac. Cons. Biol.* **2**: 279–85.
- Abensperg-Traun, M., Atkins, L., Hobbs, R. J. and Steven, D., 1998. Exotic plant invasion and understorey species richness: a comparison of two types of eucalypt woodland in agricultural Western Australia. *Pac. Cons. Biol.* **4**: 21–32.
- Abensperg-Traun, M. and Smith, G. T. (in press). How small is too small for small animals? Four terrestrial arthropod species in different-sized remnant woodlands in agricultural Western Australia. *Biodiv. Cons.* **8**.
- Abensperg-Traun, M., Smith, G. T., Steven, D. E. and Atkins, L. (in press). Different woodland types, different grazing effects? Plants and soil and litter arthropods in remnant woodlands in the Western Australian wheatbelt. *In* Temperate Eucalypt Woodlands in Australia: Biology, Conservation, Management and Restoration ed by R. J. Hobbs and C. Y. Yates. Surrey Beatty & Sons, Chipping Norton.
- Arnold, G. W. and Weeldenburg, J. R., 1991. The Distribution and Characteristics of Remnant Native Vegetation in Parts of the Kellerberrin, Tammin, Trayning and Wyalkatchem Shires of Western Australia. Technical Memorandum No. 33. CSIRO. Division of Wildlife and Ecology, Perth.
- Beard, J. S., 1980. The Vegetation of the Kellerberrin Area. Vegetation Survey of Western Australia. Vegmap Publications, Perth.
- Brian, M. V. (ed), 1978. Production Ecology of Ants and Termites. Cambridge University Press, Cambridge.
- Burrows, N., Gardiner, G., Ward, B. and Robinson, A., 1990. Regeneration of *Eucalyptus wandoo* following fire. *Aust. For.* **53**: 248–58.
- Deligne, J., Quennedey, A. and Blum, M. S., 1981. The enemies and defense mechanisms of termites. Pp. 1–76 in *Social Insects*, Vol. 2, ed by H. R. Hermann. Academic Press, New York.
- De Souza, O. F. and Brown, V. K., 1994. Effects of habitat fragmentation on Amazonian termite communities. *J. Trop. Ecol.* **10**: 197–206.
- den Boer, P. J., 1990. The survival value of dispersal in terrestrial arthropods. *Biol. Cons.* **54**: 175–92.
- Frankel, O. H. and Soulé, M. E., 1981. Conservation and Evolution. Cambridge University Press, Cambridge.
- Gay, F. J. and Wetherley, A. H., 1970. The population of a large mound of *Nasutitermes exitiosus* (Hill) (Isoptera: Termitidae). *J. Aust. Entomol. Soc.* **9**: 27–30.
- George, R., McFarlane, D. J. and Speed, R. J., 1995. The consequences of a changing hydrological environment for native vegetation in southwestern Australia. Pp. 9–22 in *Nature Conservation 4: The Role of Networks* ed by D. A. Saunders, J. L. Craig and E. M. Mattiske. Surrey Beatty & Sons, Chipping Norton.
- Greaves, T., 1967. Experiments to determine the populations of tree-dwelling colonies of termites (*Coptotermes acinaciformis* (Froggatt) and *C. frenchi* Hill). CSIRO, Division of Entomology Technical Paper No. 7, Melbourne.
- Hanski, I. and Simberloff, D., 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pp. 5–26 in *Metapopulation Biology: Ecology, Genetics, and Evolution* ed by I. A. Hanski and M. E. Gilpin. Academic Press, New York.
- Hill, G. F., 1942. Termites (Isoptera) from the Australian Region. CSIR, Melbourne.
- Hobbs, R. J., 1987. Disturbance regimes in remnants of natural vegetation. Pp. 233–40 in *Nature Conservation: The Role of Remnants of Native Vegetation* ed by D. A. Saunders, G. W. Arnold, A. A. Burbidge and A. J. M. Hopkins. Surrey Beatty & Sons, Chipping Norton.
- Hobbs, R. J., 1993. Can revegetation assist in the conservation of biodiversity in agricultural areas? *Pac. Cons. Biol.* **1**: 29–38.
- Hobbs, R. J. and Saunders, D. A., 1991. Reintegrating fragmented landscapes — a preliminary framework for the Western Australian wheatbelt. *J. Environ. Manage.* **33**: 161–67.
- Holt, J. A., Robertson, L. N. and Radford, B. J., 1993. Effects of tillage and stubble residue treatments on termite activity in two central Queensland vertosols. *Aust. J. Soil Res.* **31**: 311–17.
- Lefroy, E. C., Hobbs, R. J. and Scheltema, M., 1993. Reconciling agriculture and nature conservation: toward a restoration strategy for the Western Australian wheatbelt. Pp. 243–57 in *Nature Conservation 3: Reconstruction of Fragmented Ecosystems* ed by D. A. Saunders, R. J. Hobbs and P. R. Ehrlich. Surrey Beatty & Sons, Chipping Norton.
- Lenz, M. and Barrett, R. A., 1982. Neotenic formation in field colonies of *Coptotermes lacteus* (Froggatt) in Australia, with comments on the roles of neotenic in the genus *Coptotermes* (Isoptera: Rhinotermitidae). *Sociobiol.* **7**: 47–59.
- Lobry de Bruyn, L. A. and Conacher, A. J., 1995. Soil modification by termites in the central wheatbelt of Western Australia. *Aust. J. Soil Res.* **33**: 179–93.
- MacArthur, R. H. and Wilson, W. O., 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.



- Main, A. R., 1987. Management of remnants of native vegetation — a review of the problems and the development of an approach with reference to the wheatbelt of Western Australia. Pp. 1–13 in *Nature Conservation: the Role of Remnants of Native Vegetation* ed by D. A. Saunders, G. W. Arnold, A. A. Burbidge and A. J. M. Hopkins. Surrey Beatty & Sons, Chipping Norton.
- Majer, J. D. and Nicholls, O. G., 1998. Long-term recolonization patterns of ants in Western Australian rehabilitated bauxite mines with reference to their use as indicators of restoration success. *J. Appl. Ecol.* **35**: 161–82.
- Majer, J. D. and Delabie, J. H. C. (in press). Impact of tree isolation on arboreal and ground ant communities in cleared pasture in the Atlantic rain forest region of Bahia, Brazil. *Insect. Sociaux*.
- Majer, J. D., Recher, H. and Keals, N. (in press). Canopy arthropods in fragmented landscapes. In *Temperate Eucalypt Woodland in Australia: Biology, Conservation, Management and Restoration* ed by R. J. Hobbs and C. J. Yates. Surrey Beatty & Sons, Chipping Norton.
- McArthur, W. M., 1991. Reference Soils of South-Western Australia. Department of Agriculture, Perth, Western Australia.
- McArthur, W. M., 1993. History of landscape development. Pp. 10–22 in *Re-Integrating Fragmented Landscapes: Towards Sustainable Production and Nature Conservation* ed by R. J. Hobbs and D. A. Saunders. Surrey Beatty & Sons, Chipping Norton.
- Nutting, W. L., 1969. Flight and colony foundation. Pp. 233–82 in *Biology of Termites* ed by K. Krishna and F. M. Weesner. Academic Press, New York.
- Saunders, D. A., Hobbs, R. J. and Arnold, G. W., 1993. The Kellerberrin project on fragmented landscapes. *Biol. Cons.* **64**: 185–92.
- Simberloff, D., 1997. Biogeographic approaches and the new conservation biology. Pp. 275–84 in *The Ecological Basis of Conservation* ed by S. T. A. Pickett, R. S. Ostfeld, M. Shachak and G. E. Likens. Chapman and Hall, New York.
- Smith, G. T., 1998. Density of the burrowing scorpion *Urodacus armatus* (Scorpiones; Scorpionidae) in relation to vegetation types: implications for population decline following agricultural clearing. *Pac. Cons. Biol.* **4**: 209–14.
- Watson, J. A. L. and Gay, F. J., 1991. Isoptera (Termites). Pp. 330–47 in *The Insects of Australia* ed by Division of Entomology, CSIRO, Canberra. Melbourne University Press, Melbourne.
- Watson, J. A. L., Lendon, C. and Low, B. S., 1973. Termites in mulga lands. *Trop. Grassl.* **7**: 121–26.
- Wilson, A. D., 1990. The effect of grazing on Australian ecosystems. *Proc. Ecol. Soc. Aust.* **16**: 235–44.
- Wood, T. G. and Johnson, R. A., 1986. The biology, physiology, and ecology of termites. Pp. 1–68 in *Economic Impact and Control of Social Insects* ed by S. B. Vinson. Praeger, USA.
- Wood, T. G. and Lee, K. E., 1971. Abundance of mounds and competition among colonies of some Australian termite species. *Pedobiol.* **11**: 341–66.