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The plant pathogen *Phytophthora cinnamomi* influences habitat use by the obligate nectarivore honey possum (*Tarsipes rostratus*)

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Abstract

Introduced plant pathogens can devastate susceptible plant communities, and consequently impact on animal communities reliant on plants for food and habitat. Specifically, plant pathogens change the floristic diversity of vegetation communities, thereby reducing availability of food sources for fauna (e.g. pollen and nectar) and result in major changes to habitat structure when canopy and understorey plant species succumb to disease. *Phytophthora cinnamomi* poses a threat to flowering plant species (e.g. *Banksia* species) which are important food sources for nectarivorous fauna. The honey possum (*Tarsipes rostratus*) is the only obligate nectarivorous non-flying mammal living on a restrictive diet of nectar and pollen; consequently, these tiny mammals are likely to be particularly vulnerable to the landscape-wide devastation caused by *P. cinnamomi*. We investigated habitat selection by honey possums in a vegetation community infested with *P. cinnamomi* to determine how these mammals respond to habitat affected by this pathogen. Over four seasons, 18 honey possums were fitted with radio-transmitters and tracked to identify habitat preferences. Vegetation surveys were compared for locations selected by honey possums (as determined from tracking) and randomly selected sites. Radio-tracking revealed that sites selected by honey possums were significantly taller, denser, and more floristically diverse than their paired random locations. The presence of *P. cinnamomi* influences habitat use by honey possums, but animals show resilience in terms of using the best of what is available in both *P. cinnamomi*–affected and unaffected locations. Habitat patches comprising less susceptible species, or plants that have yet to succumb to infection, provide refuge and food resources for honey possums. Management to reduce the spread of existing *P. cinnamomi* infestations and prevent contamination of new locations will benefit vegetation communities and associated faunal communities, while identifying honey possum food plant species that are resilient to the pathogen may support revegetation attempts.

Additional keywords: *Banksia plumosa*, dieback, diet, food plants, habitat selection, pollination, VHF tracking.

Introduction

Plant pathogens can markedly alter the composition and habitat structure of native vegetation assemblages (Shearer *et al*. 2009). Coupled with ongoing climatic changes, including drought, heatwaves and frosts (Allen *et al*. 2010; Brouwers *et al*. 2013; Matusick *et al*. 2014), introduced plant pathogens put even greater stress on native plant communities (Jurskis 2005). Changes to plant communities will consequently influence fauna dependent on plants for food and habitat (Newell and Wilson 1993; Garkaklis *et al*. 2004). Therefore, identifying the impact that invasive species have on native communities is critically important for directing future management priorities (Pyšek and Richardson 2010).

Phytophthora cinnamomi, a soil-borne water mould introduced to Australia, is widely distributed around the world (Zentmyer 1988) and has been implicated in declines of native plant communities and agriculture. To date, the direct impact of *P. cinnamomi* on floristic communities has been a major focus of research (e.g. Wills 1993; Shearer *et al*. 2007, 2009, 2012). For example, the south-west botanical province in Western Australia has been a particular area of interest as the region is internationally recognised for its high level of endemic floristic and faunal diversity (Myers *et al*. 2000), both of which are at risk as a result of *P. cinnamomi* infestations (Shearer *et al*. 2007). An estimated 40% of 5710 plant species in south-west Western Australia are recognised as susceptible to this pathogen, with a further 14% of species recognised as being highly susceptible (Shearer *et al*. 2004), resulting in substantial change to floristic community structure and composition in the presence of *P. cinnamomi* (Kennedy and Weste 1986; Shearer *et al*. 2009). Most notably, *P. cinnamomi*–infested sites show a loss of flowering plant species that have large inflorescences that would support nectar-feeding animals, and a greater number of herbaceous plants (Shearer *et al*. 2009).

Major changes to the structure and diversity of affected plant communities will therefore impact fauna that rely on susceptible plants for food and habitat (Garkaklis *et al*. 2004). Volant nectarivores, such as birds and bats, to a certain extent can move in response to flower resources (McFarland 1986; Law 1993), and consequently bird communities present in healthy sites differ from those observed in *P. cinnamomi*–affected sites, where flowering plants are less plentiful (Davis *et al*. 2014). For non-volant fauna, *P. cinnamomi* can pose a greater risk to wildlife species. For example, carnivorous *Antechinus* species are observed less frequently in *P. cinnamomi*–affected areas, where preferred habitat plants have been lost and changes to vegetation structure and density are evident (Newell and Wilson 1993; Laidlaw and Wilson 2006; Armistead 2008). Also, fewer native truffles are found in *P. cinnamomi*–affected sites, which affects mycophagous *Rattus* species (Whelan 2003). Animals that are directly dependent on flowering plants for food are likely to be even more susceptible.

The honey possum (*Tarsipes rostratus*) is a small (7–16 g) marsupial endemic to south-west Western Australia. These mammals are highly specialised to feed exclusively on nectar and pollen, necessitating habitat with high floristic diversity that provides sufficient food throughout the year (Wooller *et al*. 1981; Wooller *et al*. 1993). Honey possums primarily feed on flowering plants belonging to the families Proteaceae, Myrtaceae and Epacridaceae (Wooller *et al*. 1984) with *Banksia*, *Adenanthos* and *Beaufortia* species occurring in the diet of honey possums at different study sites (Saffer 1998; Bradshaw *et al*. 2007; Dundas *et al*. 2013). An adult honey possum, weighing an average of 9 g, needs to consume 7 mL nectar and 1 g pollen each day to maintain condition (Bradshaw and Bradshaw 1999). The restrictive dietary niche of the honey possum, coupled with limited capabilities to disperse over large distances (Garavanta *et al*. 2000; Bradshaw and Bradshaw 2002), makes this small marsupial particularly vulnerable to *P. cinnamomi* infestation. The aim of this research was therefore to determine whether the presence of *P. cinnamomi* influences habitat preference by honey possums. We predicted that honey possums would preferentially avoid using *P. cinnamomi*–affected vegetation because of the reduced number of flowering plants present at these sites compared with intact vegetation.

Methods

Study site

The study was carried out in a coastal banksia heathland along the south-west coast, Western Australia (Fig. 1). The vegetation assemblages at the study site comprise a floristically diverse range of low-lying, dense shrubs which cover the ground. The site is surrounded by spongelite ridges, which are characterised by an abundance of *Banksia*, *Eucalyptus* and *Hakea* species (Mercer and Leighton 1999). Deep sand deposits in the low-lying areas support *Banksia baxteri* thickets (Mercer and Leighton 1999) and the dense scrub is dominated by *Banksia*, *Adenanthos* and *Beaufortia* species. (Fig. 2*a*). The dominant banksia species at the site are *B. baxteri*, which forms taller (~2 m) thickets, and dense shrub banksias, *B. nutans* and *B. plumosa plumosa*. The climate across south-west Western Australia is typically Mediterranean, with cool, wet winters and warm, dry summers. The study site is within a proposed conservation park near Cape Riche, 119 km north-east of Albany (–34.567397°, 118.712249°), and was selected because it has a known honey possum population and a patchy mosaic of *P. cinnamomi*–affected and intact habitat. *P. cinnamomi* was introduced into the study site sometime during the 1980s, when bush tracks were created by commercial flower pickers harvesting *Banksia coccinea* and *B. baxteri* flowers (Mercer and Leighton 1999). Samples of dying plants were plated onto a *Phytophthora*-specific agar (Hüberli *et al*. 2000) and the presence of *P. cinnamomi* in the study area was confirmed (data not presented).

Honey possum trapping

Trapping and radio-tracking of honey possums was carried out over four two-week-long field trips during 2007 (Summer: 28 January – 9 February; Autumn: 29 April – 11 May; Winter: 5–17 August; Spring: 18–30 November). A total of 60 pitfall traps that consisted of 40-cm lengths of 15-cm-diameter stormwater PVC pipe were buried up to the rim so they sat flush with the ground. The traps were placed along three 100-m-long transect lines that ran perpendicular to a *P. cinnamomi* disease front, with 10 traps located in *P. cinnamomi*–affected habitat and 10 traps located in unaffected habitat (Fig. 1). The traps were located in pairs, connected by 30-cm-tall aluminium wire mesh drift fencing placed 5 m either side of each trap with the orientation of the drift fences alternating perpendicular angles (Dundas *et al*. 2013). The three 'trapping' transects were spaced 180–400 m apart. On the basis of previous trapping data (Garavanta *et al*. 2000), we originally believed this spacing would provide three separate replicates; however, the distances over which we tracked animals moving (see Results) clearly indicated that these transects were not independent and therefore we do not compare the data for each trapping site, but instead treat all three replicates as a single study population.

Honey possum radio-tracking

Honey possums are crepuscular (Arrese and Runham 2001) and therefore traps were opened just before dusk and were checked at first light. All captured possums were weighed, their noses swabbed for pollen to determine food plants (Dundas *et al*. 2013) and the animals were ear punched to enable identification of individuals. Honey possums weighing <7 g were classified as juveniles and those >7 g were classified as adults (Garavanta 1997).

To observe habitat preferences, 18 honey possums (>5.9 g body mass, females that did not have pouch young present) were fitted with 0.36-g LB-2N and 0.9-g LD-2 radio-transmitters (Holohil

Systems Ltd, Canada). The number of honey possums tracked each month varied. Given the very short battery life of the transmitters (~12 days for the 0.36-g LB-2N and ~45 days for the 0.9-g LD-2), transmitters were temporarily fixed to honey possums with a combination of superglue in both gel and liquid forms (Selleys Pty Ltd, Australia). We initially found transmitter attachment to be problematic in some instances, with transmitter attachment particularly short-lived for cool weather where the glue was slow to dry. In-house tests were subsequently carried out in a cool room (~5°C) with a variety of glues to determine which product adhered best in cooler temperatures. It was concluded that a combination of Selleys non-drip gel (which is slower drying but holds the transmitter in place) applied first with the transmitter followed by Selleys liquid gel (which dries quickly but does not stick if the animal moves when the transmitter is being attached) applied around the transmitter was the most effective solution.

For attachment, the fur above the shoulder blades was trimmed with scissors before an application of superglue, followed by the transmitter. Honey possums were fitted with transmitters early in the morning (between 0600 and 0800 hours, depending on first light) when pit traps were checked around dawn. Following transmitter application, honey possums were placed in a calico bag for up to 15 min to allow the glue to dry before being released at point of capture. Observations of individuals captured later, after their transmitter had fallen off, showed that the patches of superglue simply peeled off and did not damage the underlying skin.

Locations of radio-tracked honey possums were determined using a triangulation method that employed two researchers with hand-held receivers and antennae (Kenward 2001) that enabled habitat selection to be determined while minimising disturbance. Radio-tracked honey possums were triangulated to within 1–2 m of their location but were not often observed. Locations where honey possums were observed to be ‘on the move’ were excluded from analyses. The first location for each radio-tracked honey possum after transmitter attachment was recorded mid- to late-afternoon the day of release, which was necessitated by the limited range of the transmitters (ensuring that the animal had not moved too far from the point of release before it was located). Thereafter, tracking was carried out 2–3 times after dusk and 1–2 times during the day over subsequent days until the transmitter detached (determined as more than two consecutive locations at the same site, whereupon the area was searched intensively to retrieve the transmitter). During the summer months, most tracking was conducted during the evening when honey possums are considered to be most active (Garavanta 1997; Russell and Renfree 1989). During the winter months, honey possums were also tracked during the day as individuals tended to move further (presumably in search of food) and would go out of range if not tracked frequently. In winter, animals were sometimes located in vegetation where they often remained in torpor when approached (Fig. 2*c*).

GPS coordinates for honey possum locations collected during radio-tracking were processed using Garmin BaseCamp 4.2.3 (Garmin Ltd). Routes were created for each honey possum from the original capture location to the last location recorded. The total distance travelled is a cumulative total of the direct (straight) distance between recorded locations. Average distances moved by tracked honey possums is the total distance divided by the total number of locations.

Vegetation surveys

The locations of radio-tracked honey possums were marked with flagging tape and GPS logged. These honey possum–selected locations ($n = 77$) were compared with stratified locations randomly selected within the landscape ($n = 45$) and representative of all habitat types in the study area. At a later time, vegetation at each location was surveyed in daylight. Vegetation density was measured with a touch pole marked at 10-cm intervals by counting vegetation touches at each 10-cm interval. A 3-m-diameter circle was marked off around the location and the pole was placed in random places within this circle 10 times for each honey possum location or 5 times for the random locations. The average number of touches was calculated at each height for each location, and the same data were used to estimate average vegetation height. Percentage vegetation cover was estimated by visual assessment. The presence of each of four main honey possum food plant species (Dundas *et al*. 2013) – *B. p. plumosa*, *Adenanthos cuneatus*, *B. nutans* and *Beaufortia anisandra* – were recorded for each location. Locations were categorised as affected by *P. cinnamomi* (within the area demarcated by contrasting vegetation change with unaffected vegetation) or not affected (outside this affected area);

only locations that could be conclusively defined as unaffected or affected were included in the analyses (22 of 144 locations sampled were excluded).

Data analysis

A Mann–Whitney U test was conducted to determine whether there was a significant difference between the average distance travelled by honey possums in relation to sex, season and weight of transmitter. A Spearmann Rank order correlation was conducted to determine whether average distance moved was correlated with body mass of tracked honey possums.

Non-metric multidimensional scaling (MDS) was conducted using Bray–Curtis similarity measures to visualise differences in vegetation density (number of touches) with location categories – selection (honey possum–selected versus random locations) and *P. cinnamomi* presence (*P. cinnamomi*–affected versus unaffected locations) – as independent factors. Two-dimensional MDS graphs provide a visual representation of the rank order of locations where relative distances between points indicate relative dissimilarity between locations (Clarke and Warwick 1994). The MDS was followed by a two-way NPMANOVA to test for effects of selection and *P. cinnamomi* presence as independent factors and then SIMPER analysis to determine which vegetation height contributed the greatest dissimilarity to the vegetation classes (PAST: Hammer *et al*. 2001).

To investigate where the difference in vegetation structure lay, we tested several measures as dependent factors in subsequent analyses. For each location, Shannon's Diversity Indices were calculated to quantify the spread of vegetation structure (structural complexity), and averages were calculated for mean vegetation height, percentage vegetation coverage, number of touches for 0–230 cm, and number of touches for 40–140 cm (as significant differences were calculated for this height range between location categories). Data were square-root transformed prior to analysis. These measures were compared by factorial ANOVA with selection (honey possum selected and random) and *P. cinnamomi* presence as independent factors. *Post hoc* Tukey unequal-*n* HSD tests were calculated to compare differences between the four location categories (i.e. honey possum–selected affected, honey possum–selected unaffected, random affected and random unaffected).

The presence of the four main honey possum food plant species was compared between selected versus random sites, or *P. cinnamomi*–affected versus unaffected sites, by Chi-square test, with expected values calculated assuming an equal proportion of these plants across all sites.

Values are presented as means ± 1 s.d. and data analyses were carried out in STATISTICA (Statsoft Inc. 2006).

Results

The success of transmitters remaining attached to animals varied markedly (4 h to 9 days). Two transmitters had fallen off within 30 min of attachment and therefore no tracking data were obtained (TR10 and TR14). Of the remaining 16, half were attached to males and half females. Of the 18 tracked honey possums (average body mass = 8.31 ± 2.43 g; range = 5.9–16 g), four or more location fixes were obtained for 12 animals (Table 1). Average distances moved between locations were not different between the sexes (Mann–Whitney U test: $Z_{8,8} = 0.84$, $P = 0.40$) and were not correlated with honey possum body mass (Spearman Rank Order Correlation: $R_s = 0.06$, $P > 0.05$). There were no seasonal differences in average tracking distance (Median test: $\chi^2_3 = 1.83$, $P = 0.608$), or weight of the transmitter and the average tracking distance (Mann–Whitney U test: $Z_{2,14} = –0.16$, $P = 0.874$).

Honey possum–selected locations were significantly different from random locations in terms of vegetation structure, density, and composition. Honey possums select taller, denser vegetation within the landscape (two-way NPMANOVA: $F_{1,118} = 16.34$, $P < 0.001$; two dimensional MDS plot: Fig. 3). *P. cinnamomi*–affected locations (either random or honey possum–selected) were significantly different from unaffected locations in terms of vegetation density ($F_{1,118} = 13.61$, $P < 0.001$). The honey possum–selected × *P. cinnamomi*–affected interaction term was not statistically significant ($F_{1,118} = –11.75$, $P = 0.735$). The greatest contribution to the difference between honey possum–selected versus random locations was determined by the 10-cm height category (9.31% of variance explained), followed by vegetation between 20 and 70 cm (total 51.17% of variance) (SIMPER analyses). Taller vegetation showed a weaker contribution to this difference. The same pattern was observed for the difference in vegetation structure for *P. cinnamomi*–affected versus unaffected vegetation.

Breaking these measures down into more specific measures of habitat structure, tracked honey possums actively selected areas with vegetation that was significantly taller ($F_{1,118} = 11.46$, $P < 0.001$), denser (percentage vegetation coverage ($F_{1,118} = 5.68$, $P = 0.019$), as well as touchpole estimates for 0–230 cm ($F_{1,118} = 47.56$, $P < 0.001$) and 40–140 cm ($F_{1,118} = 41.29$, $P < 0.001$)), and had greater structural complexity ($F_{1,118} = 54.00$, $P < 0.001$) than vegetation in the general study area (as represented by the randomly surveyed locations) (Fig. 4; Table 2).

Habitat structure in *P. cinnamomi*–affected vegetation in both selected and random locations was significantly shorter ($F_{1,118} = 21.57$, $P < 0.001$), less dense (percentage vegetation coverage ($F_{1,118} = 9.88$, $P = 0.002$) and touchpole estimates from 0–230 cm ($F_{1,118} = 18.74$, $P < 0.001$) and 40–140 cm ($F_{1,118} = 24.83$, $P < 0.001$)) and structurally less complex ($F_{1,118} = 42.70$, $P < 0.001$) than healthy vegetation.

B. p. plumosa was recorded less often at the *P. cinnamomi*–affected sites ($\chi^2_1 = 9.23$, $P = 0.002$), but was not significantly different between the honey possum–selected compared with the random locations ($\chi^2_1 = 1.05$, $P = 0.306$). *B. p. plumosa* was located in 70% of unaffected honey possum–selected sites (Table 3). The incidence of the other three food plant species was not significantly different between the selected versus random sites, or the *P. cinnamomi*–affected versus unaffected sites.

Discussion

Honey possums preferentially selected taller, denser vegetation within the landscape and were found to use both *P. cinnamomi*–affected and healthy vegetation. Radio-tracked animals were frequently observed using *B. p. plumosa*, a plant species that is susceptible to *P. cinnamomi* infestation and found less frequently in affected sites. Honey possums can move relatively long distances to seek out food plants.

Distribution of Phytophthora cinnamomi in relation to areas utilised by honey possums

Changes to habitat structure and composition as a result of *P. cinnamomi* infestation are significant, with affected plant species being replaced by a different vegetation complex dominated by non-susceptible species (Kennedy and Weste 1986; Shearer *et al*. 2009). Honey possums persist around the *P. cinnamomi* site examined, with tracked animals actively selecting areas with vegetation significantly taller, denser, and with greater structural complexity than vegetation in the general study area.

The distribution of *P. cinnamomi* at Cape Riche is patchy with small 'islands' of less susceptible species (e.g. *Eucalyptus angulosa*) persisting within affected areas. These vegetation islands within *P. cinnamomi*–affected habitat provide food resources and suitable refuge for honey possums, breaking up the distances that animals would have to travel across *P. cinnamomi*–affected sites. In the presence of fire at the nearby Fitzgerald River National Park, honey possums showed a similar dependence on unaffected patches of vegetation, where pollen sampling indicated that animals captured in burnt sites were also foraging in nearby unburnt patches (Everaardt 2003). This demonstrates how well these tiny marsupials are able to move across the landscape in search of nectar and pollen. Heterogeneity in the effects of infestation by plant pathogens such as *P. cinnamomi* is likely to be important for persistence of several other mammal species. In the Brisbane Ranges, Victoria, islands of unaffected vegetation in *P. cinnamomi*–affected areas tend to be surrounded by bare ground, restricting the movements of small mammal species dependent on dense vegetation (Newell and Wilson 1993). In widespread areas of *P. cinnamomi* infestation, these patches of healthy vegetation are clearly important and are also likely to be providing refuge for other species captured at the site (e.g. ash-grey mouse (*Pseudomys albocinereus*) and grey-bellied dunnart (*Sminthopsis griseoventer*)).

Impact of the Phytophthora pathogen on fauna

Loss of susceptible plant species used for food and refuge poses a threat to honey possums in affected habitats. Five of nine plant species most frequently visited by honey possums, as determined from pollen sampling, are known to be susceptible to *P. cinnamomi* (Dundas *et al*. 2013). In the short term, honey possums seem to be opportunistic and will exploit less susceptible species (in lieu of more frequently visited flowering plants) as well as individual plants that have not yet succumbed to the pathogen. Honey possums also exhibited long-range foraging trips to exploit food sources. In summer, a honey possum was tracked to a clump of *E. angulosa* that was 254 m from the previous fix taken only 5 h before. Another individual moved beyond the range of the transmitters (i.e. more than 250 m) in the space of 2 h, but then had returned to the central part of the research site by early morning the next day. Similar observations were made for honey possums in Scott National Park, where an individual travelled more than 1 km to reach a stand of flowering *Banksia occidentalis* (Bradshaw *et al*. 2007). At Mount Lesueur Nature Reserve, female honey possums fitted with 0.4-g transmitters during summer moved 20–80 m between successive location fixes while males moved 50–200 m between fixes (Arrese and Runham 2001). In winter, honey possums moved almost double this distance (Arrese and Runham 2001), presumably to seek out scarcer food resources. The necessity for honey possums to move longer distances to seek out food resources may be facilitating dispersal to new areas (Clancy 2011).

These observations of long-distance movements contradict previous observations of sedentary honey possums that rarely moved more than 30 m between trap capture sites, as determined from a 12-year pitfall mark–recapture survey in the Fitzgerald River National Park (Garavanta *et al*. 2000). The present study radio-tracked over a relatively short period (a 1-year study with four trapping and tracking sessions), and the information about habitat preference and reliance upon vegetation could not have been established from trapping alone.

The presence of *P. cinnamomi* not only results in the loss of floristic diversity and compromises year-round food availability, but also results in loss of suitable refuge for fauna. Honey possums enter a torpid state during cooler weather when food resources are low (Withers *et al*. 1989), which would make them easy prey if dense vegetation were no longer available. In the current study, radio-tracking revealed that dense *B. p. plumosa* shrubs were regularly used by honey possums for both food and refuge (Fig. 2*c*). For other small mammal species, *P. cinnamomi* threatens plant species that provide preferred habitat components. For example, *Antechinus stuartii* was captured less frequently in *P. cinnamomi*–affected habitats in Victoria, owing to the loss of susceptible *Xanthorrhoea australis* plants (Newell and Wilson 1993). A similar trend was observed for *A. flavipes* in Western Australia, where animals were detected less frequently in affected habitats where *Xanthorrhoea preissii* (used for refuge) was generally absent (Armistead 2008).

Conversely, the loss of mature oak trees in native forests infected with *Phytophthora ramorum* (the causative agent of sudden oak death, SOD) in California, USA, actually created more favourable habitat for small mammals, at least in the short term (10 years after infection) (Tempel and Tietje 2006). Dusky-footed woodrats (*Neotoma fuscipes*), brush mice (*Peromyscus boylii*) and California mice (*Peromyscus californicus*) were more abundant in diseased forests as loss of trees infected with *P. ramorum* pathogen changed the habitat structure and resulted in increased shrub cover, more coarse woody debris and low tree densities, which were favourable to small mammals (Tempel and Tietje 2006). Similarly in the San Francisco Bay area in California, the presence of deer mice (*Peromyscus maniculatus*) and western fence lizards (*Sceloporus occidentalis*) was positively correlated with forests disturbed by SOD although, conversely, the presence of dusky-footed woodrats was negatively correlated with SOD disturbance at this site (Swei *et al*. 2011).

Conclusion and management implications

This study provides a valuable source of information that is directly applicable to small mammal conservation management in *Banksia* heathlands infested with *P. cinnamomi*. The presence of *P. cinnamomi* clearly influences habitat use by honey possums, although the animals show resilience in terms of how they make use of resources across the landscape, using the best habitat available within and around infested areas. This information gives conservation managers further incentive to ensure that *P. cinnamomi*–affected areas are kept disease-free while further spread within affected areas is minimised. Ideally, eradication of the pathogen from sensitive sites and preventing further spread is the key to protecting susceptible plant communities and the animals that depend upon them. The application of phosphite has shown promise for controlling this pathogen and inducing resistance in susceptible species (Hardy *et al*. 2001) with successful eradication experiments having been carried out at the Cape Riche site (Dunstan *et al*. 2010). Restriction of vehicle movements in wet conditions and suitable hygiene to remove soil from shoes, tyres and equipment before entering a disease-free area needs to be regularly practiced and enforced.

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References

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S. W., Semerci, A., and Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* **259**, 660–684.

Armistead, R. J. (2008). The impact of *Phytophthora cinnamomi* on the distribution of the yellow-footed antechinus (mardo) (*Antechinus flavipes leucogaster*) (Marsupialia: Dasyuridae). Ph.D. Thesis, Murdoch University, Perth.

Arrese, C., and Runham, P. B. (2001). Redefining the activity pattern of the honey possum (*Tarsipes rostratus*). *Australian Mammalogy* **23**, 169–172.

Bradshaw, S. D., and Bradshaw, F. J. (1999). Field energetics and the estimation of pollen and nectar intake in the marsupial honey possum, *Tarsipes rostratus*, in heathland habitats of south-western Australia. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* **169**, 569–580.

Bradshaw, S. D., and Bradshaw, F. J. (2002). Short-term movements and habitat use of the marsupial honey possum (*Tarsipes rostratus*). *Journal of Zoology* **258**, 343–348.

Bradshaw, S. D., Phillips, R. D., Tomlinson, S., Holley, R. J., Jennings, S., and Bradshaw, F. J. (2007). Ecology of the honey possum, *Tarsipes rostratus*, in Scott National Park, Western Australia. *Australian Mammalogy* **29**, 25–38.

Brouwers, N., Matusick, G., Ruthrof, K., Lyons, T., and Hardy, G. (2013). Landscape-scale assessment of tree crown dieback following extreme drought and heat in a Mediterranean eucalypt forest ecosystem. *Landscape Ecology* **28**, 69–80.

Clancy, R. L. (2011). The dispersal of honey possums, *Tarsipes rostratus*, in relation to habitat fragmentation and fire. Ph.D. Thesis, University of Western Australia, Nedlands.

Clarke, K. R., and Warwick, R. M. (1994). ‘Change in Marine Communities: an Approach to Statistical Analysis and Interpretation.’ (Natural Environment Research Council: Plymouth Marine Laboratory, Plymouth, UK.)

Davis, R. A., Valentine, L. E., Craig, M. D., Wilson, B., Bancroft, W. J., and Mallie, M. (2014). Impact of *Phytophthora*-dieback on birds in *Banksia* woodlands in south west Western Australia. *Biological Conservation* **171**, 136–144.

Dundas, S. J., Fleming, P. A., and Hardy, G. E. S. J. (2013). Flower visitation by honey possums (*Tarsipes rostratus*) in a coastal banksia heathland infested with the plant pathogen *Phytophthora cinnamomi*. *Australian Mammalogy* **35**, 166–174.

Dunstan, W. A., Rudman, T., Shearer, B. L., Moore, N. A., Paap, T., Calver, M. C., Dell, B., and Hardy, G. E. S. J. (2010). Containment and spot eradication of a highly destructive, invasive plant pathogen (*Phytophthora cinnamomi*) in natural ecosystems. *Biological Invasions* **12**, 913–925.

Everaardt, A. (2003). The impact of fire on the honey possum *Tarsipes rostratus* in the Fitzgerald River National Park, Western Australia. Ph.D. Thesis, Murdoch University, Perth.

Garavanta, C. A. M. (1997). A mark-recapture study of the social organisation of the honey possum *Tarsipes rostratus* in the Fitzgerald River National Park, Western Australia. Ph.D. Thesis, Murdoch University, Perth.

Garavanta, C. A. M., Wooller, R. D., and Richardson, K. C. (2000). Movement patterns of honey possums, *Tarsipes rostratus*, in the Fitzgerald River National Park, Western Australia. *Wildlife Research* **27**, 179–183.

Garkaklis, M., Calver, M., Wilson, B., and Hardy, G. E. S. J. (2004). Habitat alteration caused by an introduced plant disease, *Phytophthora cinnamomi*: a potential threat to the conservation of Australian forest fauna. In ‘Conservation of Australias Forest Fauna’. pp. 899–913. (Royal Zoological Society of New South Wales: Sydney.)

Hammer, Ø., Harper, D. A. T., and Ryan, P. D. (2001). PAST: Paleontological statistics software package for education and data analysis version 3.10. *Palaeontologia Electronica* **4**, 9.

Hardy, G. E. S. J., Barrett, S., and Shearer, B. L. (2001). The future of phosphite as a fungicide to control the soilborne plant pathogen *Phytophthora cinnamomi* in natural ecosystems. *Australasian Plant Pathology* **30**, 133–139.

Hüberli, D, Tommerup, I. C., and Hardy, G. E. S. J. (2000). False negative isolations or absence of lesions may cause mis-diagnosis of diseased plants infected with *Phytophthora cinnamomi*. *Australasian Plant Pathology* **29**, 164–169.

Jurskis, V. (2005). Eucalypt decline in Australia, and a general concept of tree decline and dieback. *Forest Ecology and Management* **215**, 1–20.

Kennedy, J., and Weste, G. (1986). Vegetation changes associated with invasion by *Phytophthora cinnamomi* on monitored sites in the Grampians, Western Victoria. *Australian Journal of Botany* **34**, 251–279.

Kenward, R. E. (2001). 'A Manual for Wildlife Radio Tagging.' (Academic Press: San Diego.)

Laidlaw, W. S., and Wilson, B. A. (2006). Habitat utilisation by small mammals in a coastal heathland exhibiting symptoms of *Phytophthora cinnamomi* infestation. *Wildlife Research* **33**, 639–649.

Law, B. S. (1993). Roosting and foraging ecology of the Queensland blossom bat (*Syconycteris australis*) in north-eastern New South Wales: flexibility in response to seasonal variation. *Wildlife Research* **20**, 419–431.

Matusick, G., Ruthrof, K. X., Brouwers, N. C., and Hardy, G. S. J. (2014). Topography influences the distribution of autumn frost damage on trees in a Mediterranean-type *Eucalyptus* forest. *Trees* **28**, 1449–1462.

McFarland, D. C. (1986). Seasonal changes in the abundance and body condition of honeyeaters (Meliphagidae) in response to inflorescence and nectar availability in the New England National Park, New South Wales. *Australian Journal of Ecology* **11**, 331–340.

Mercer, J., and Leighton, S. (1999). Cheyne Bay coastal survey: Cape Riche to Pallinup River. Report for Wellstead Land Conservation District Committee, Western Australia.

Myers, N., Mittermeier, R. A., Mittermeier, C. C., da Fonseca, G. A., and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858.

Newell, G. R., and Wilson, B. A. (1993). The relationship between cinnamon fungus (*Phytophthora cinnamomi*) and the abundance of *Antechinus stuartii* (Dasyuridae: Marsupialia) in the Brisbane Ranges, Victoria. *Wildlife Research* **20**, 251–259.

Pyšek, P., and Richardson, D. M. (2010). Invasive species, environmental change and management, and health. *Annual Review of Environment and Resources* **35**, 25–55.

Russell, E. M., and Renfree, M. B. (1989). Tarsipedidae. In 'Fauna of Australia Volume 1B'. (Ed. W. W. Walton.) pp. 769–782. (Australian Government Publishing Service: Canberra.)

Saffer, V. M. (1998). A comparison of foodplant utilisation by nectar-feeding marsupials and birds in the Fitzgerald River National Park, Western Australia. Ph.D. Thesis, Murdoch University, Perth.

Shearer, B. L., Crane, C. E., and Cochrane, A. (2004). Quantification of the susceptibility of the native flora of the South-West Botanical Province, Western Australia, to *Phytophthora cinnamomi*. *Australian Journal of Botany* **52**, 435–443.

Shearer, B. L., Crane, C. E., Barrett, S., and Cochrane, A. (2007). *Phytophthora cinnamomi* invasion, a major threatening process to conservation of flora diversity in the South-west Botanical Province of Western Australia. *Australian Journal of Botany* **55**, 225–238.

Shearer, B., Crane, C., Fairman, R., and Dunne, C. (2009). Ecosystem dynamics altered by pathogen-mediated changes following invasion of *Banksia* woodland and *Eucalyptus marginata* forest biomes of south-western Australia by *Phytophthora cinnamomi*. *Australasian Plant Pathology* **38**, 417–436.

Shearer, B., Crane, C., and Dunne, C. (2012). Variation in vegetation cover between shrubland, woodland and forest biomes invaded by *Phytophthora cinnamomi*. *Australasian Plant Pathology* **41**, 413–424.

Statsoft Inc (2006). 'STATISTICA (Data Analysis Software System). Version 7.1.'

Swei, A., Ostfeld, R. S., Lane, R. S., and Briggs, C. J. (2011). Effects of an invasive forest pathogen on abundance of ticks and their vertebrate hosts in a California Lyme disease focus. *Oecologia* **166**, 91–100.

Tempel, D. J., and Tietje, W. D. (2006). Potential effects of sudden oak death on small mammals and herpetofauna in coast live oak (*Quercus agrifolia*) woodlands. In 'Proceedings of the Sudden Oak Death Second Science Symposium: the State of Our Knowledge, Albany, California, USA'. (Eds S. J. Frankel, P. J. Shea and M. I. Haverty.) pp. 233–236.

Whelan, J. K. (2003). The impact of *Phytophthora cinnamomi* on the abundance and mycophagous diet of the bush rat (*Rattus fuscipes*). B.Sc.(Honours) Thesis, Murdoch University, Perth.

Wills, R. T. (1993). The ecological impact of *Phytophthora cinnamomi* in the Stirling Range National Park, Western Australia. *Australian Journal of Ecology* **18**, 145–159.

Withers, P. C., Richardson, K. C., and Wooller, R. D. (1989). Metabolic physiology of euthermic and torpid honey possums, *Tarsipes rostratus*. *Australian Journal of Zoology* **37**, 685–693.

Wooller, R. D., Renfree, M. B., Russell, E. M., Dunning, A., Green, S. W., and Duncan, P. (1981). Seasonal changes in a population of the nectar-feeding marsupial *Tarsipes spencerae* (Marsupialia: Tarsipedidae). *Journal of Zoology* **195**, 267–279.

Wooller, R. D., Russell, E. M., and Renfree, M. B. (1984). Honey possums and their food plants. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume.) pp. 439–443. (Surrey Beatty: Sydney.)

Wooller, R. D., Richardson, K. C., and Collins, B. G. (1993). The relationship between nectar supply and the rate of capture of a nectar-dependent small marsupial *Tarsipes rostratus*. *Journal of Zoology* **229**, 651–658.

Zentmyer, G. A. (1988). Origin and distribution of four species of *Phytophthora*. *Transactions of the British Mycological Society* **91**, 367–378.

Fig. 1. Map of study site. Inset (*a*) shows locations of trap lines at the study site and hashed area indicates *Phytophthora cinnamomi*–affected vegetation.

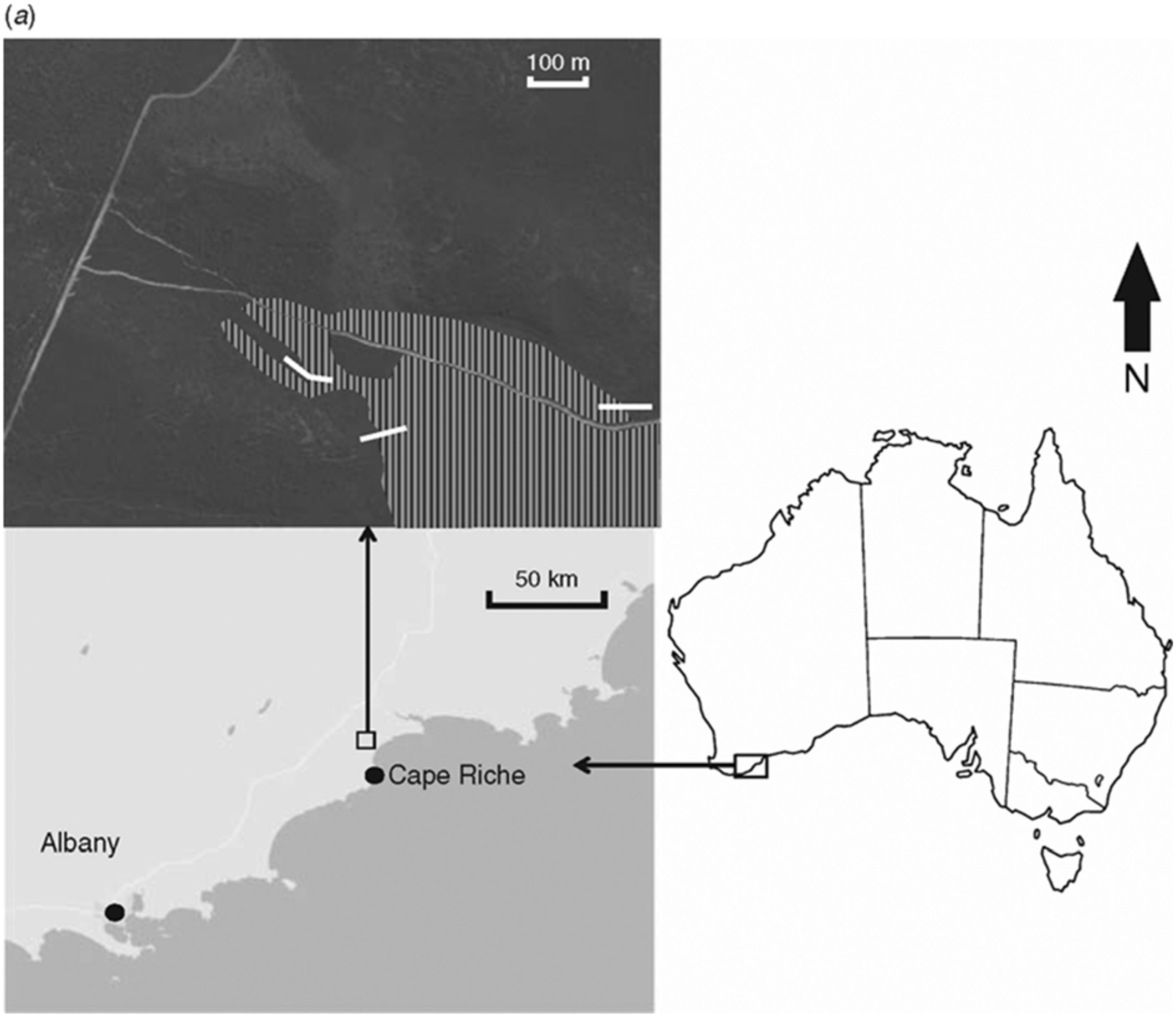


Fig. 2. (*a*) Healthy *Banksia baxteri* thicket showing presence of tall *Banksia* species and structural complexity. (*b*) *Phytophthora cinnamomi*–affected thicket characterised by low, sparse vegetation dominated and lacking many susceptible species. (*c*) A torpid honey possum tracked to a *Banksia plumosa plumosa* plant, ~1 m off the ground.

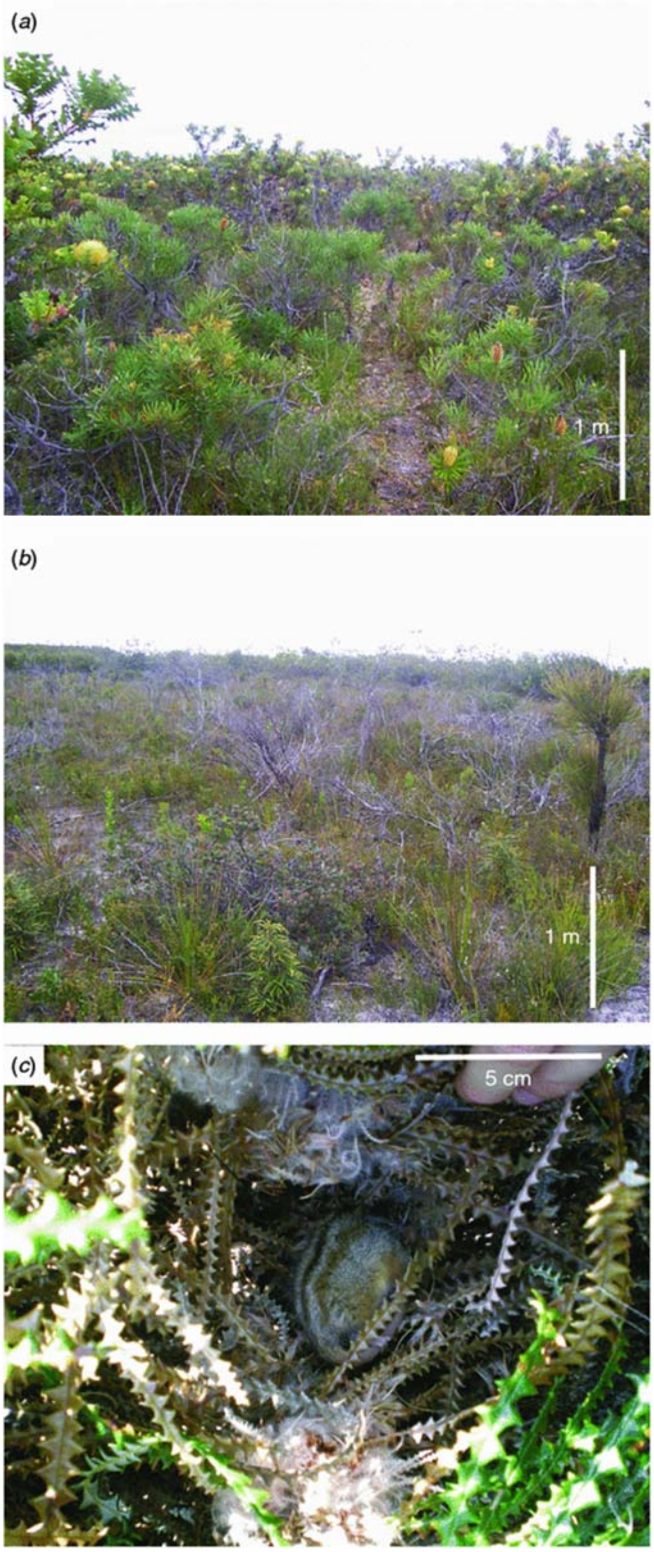


Fig. 3. Non-metric multidimensional scaling graph representing the rank order of *P. cinnamomi*–affected (PA) and unaffected (UA) locations for both honey possum–selected and random locations. The relative distances between points (which represent the locations) indicates the dissimilarity between locations.

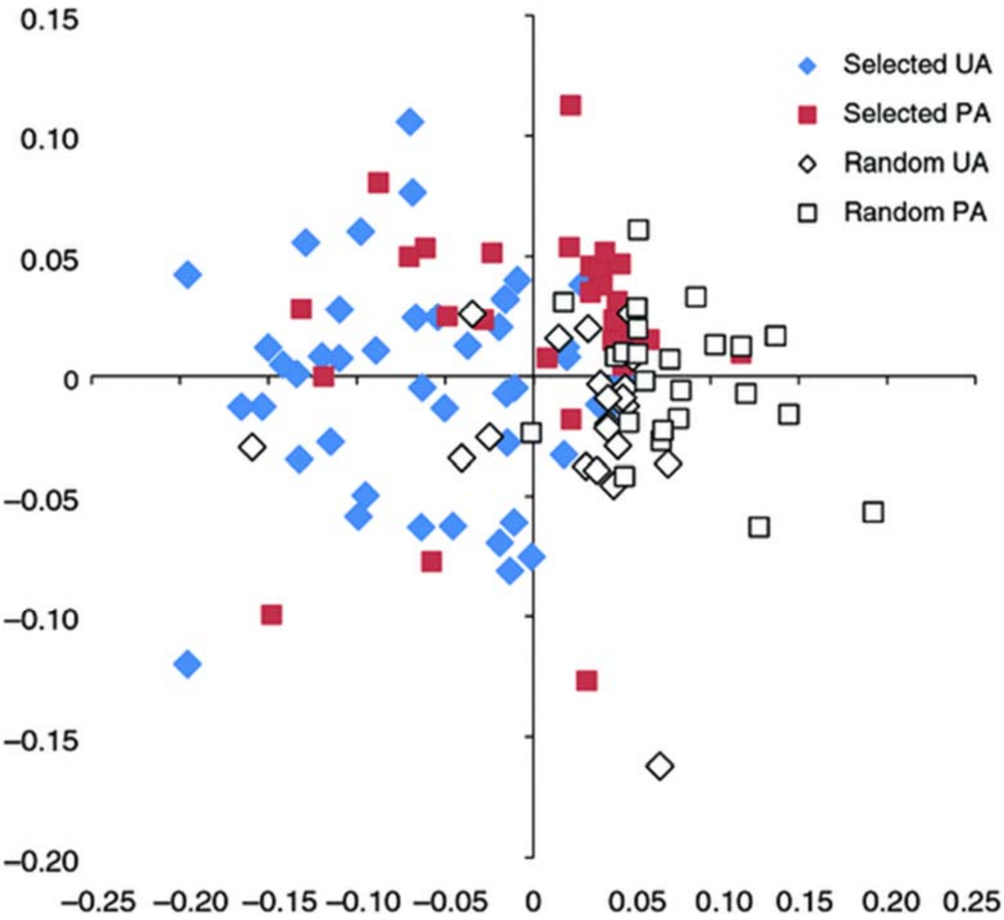


Fig. 4. Average (±1 s.d.) number of vegetation touches at height classes 0–230 cm. *n* = number of locations included for each category (excludes locations where *P. cinnamomi* status was inconclusive or where honey possums were moving). Hashes represent significant differences between affected and unaffected sites (#, $P < 0.05$; ##, $P < 0.01$; ###, $P < 0.001$), asterisks represent significant differences between honey possum–selected and random sites (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$) as determined by factorial MANOVA with Tukey's unequal-*n* HSD *post hoc* analysis (represented by letters).

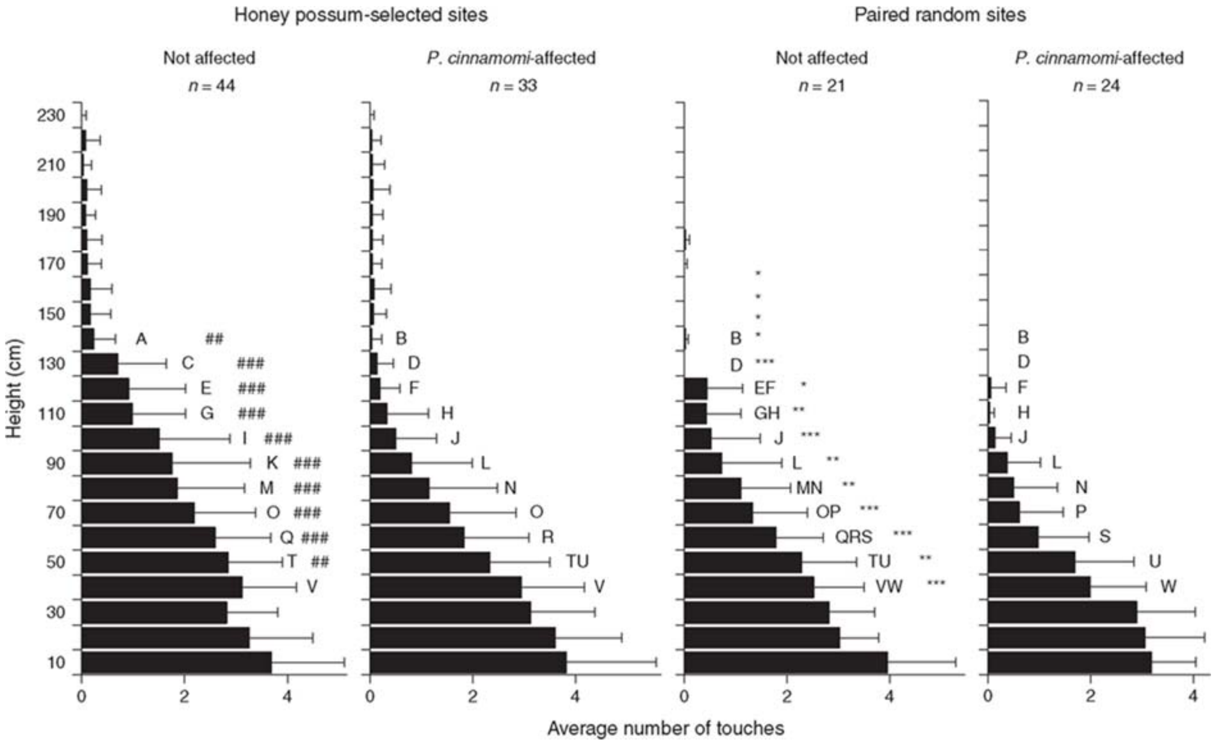
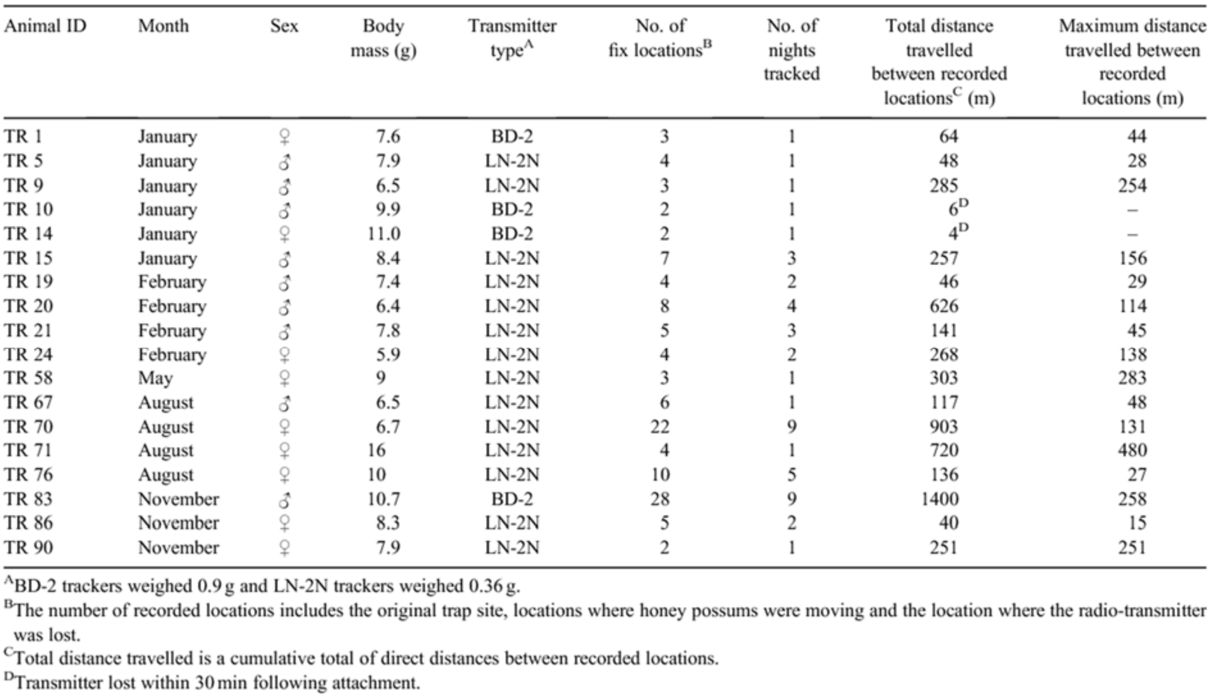


Table 1. Individual honey possums radio-tracked during the study



Animal ID	Month	Sex	Body mass (g)	Transmitter type[A]	No. of fix locations[B]	No. of nights tracked	Total distance travelled between recorded locations[C] (m)	Maximum distance travelled between recorded locations (m)
TR 1	January	♀	7.6	BD-2	3	1	64	44
TR 5	January	♂	7.9	LN-2N	4	1	48	28
TR 9	January	♂	6.5	LN-2N	3	1	285	254
TR 10	January	♂	9.9	BD-2	2	1	6[D]	–
TR 14	January	♀	11.0	BD-2	2	1	4[D]	–
TR 15	January	♂	8.4	LN-2N	7	3	257	156
TR 19	February	♂	7.4	LN-2N	4	2	46	29
TR 20	February	♂	6.4	LN-2N	8	4	626	114
TR 21	February	♂	7.8	LN-2N	5	3	141	45
TR 24	February	♀	5.9	LN-2N	4	2	268	138
TR 58	May	♀	9	LN-2N	3	1	303	283
TR 67	August	♂	6.5	LN-2N	6	1	117	48
TR 70	August	♀	6.7	LN-2N	22	9	903	131
TR 71	August	♀	16	LN-2N	4	1	720	480
TR 76	August	♀	10	LN-2N	10	5	136	27
TR 83	November	♂	10.7	BD-2	28	9	1400	258
TR 86	November	♀	8.3	LN-2N	5	2	40	15
TR 90	November	♀	7.9	LN-2N	2	1	251	251

[A] BD-2 trackers weighed 0.9 g and LN-2N trackers weighed 0.36 g.

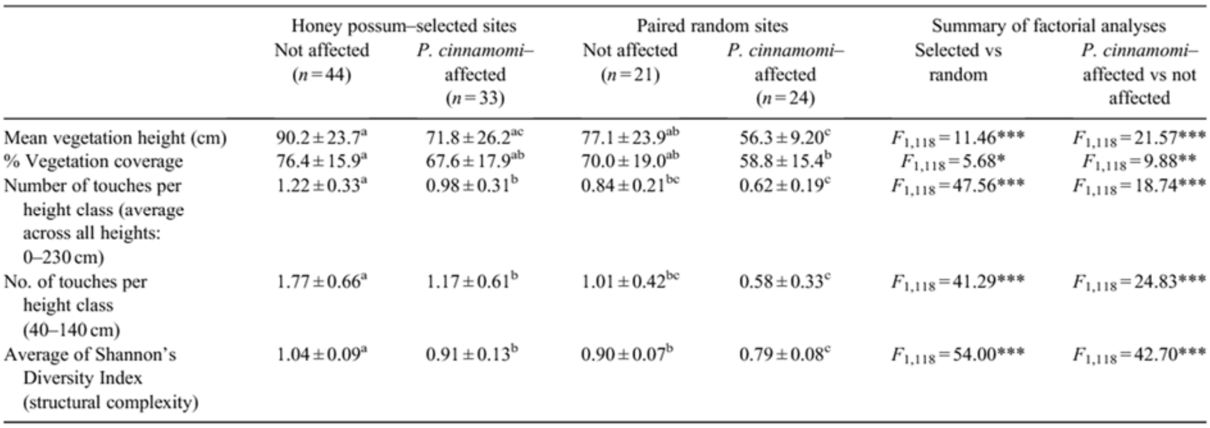
[B] The number of recorded locations includes the original trap site, locations where honey possums were moving and the location where the radio-transmitter was lost.

[C] Total distance travelled is a cumulative total of direct distances between recorded locations.

[D] Transmitter lost within 30 min following attachment.

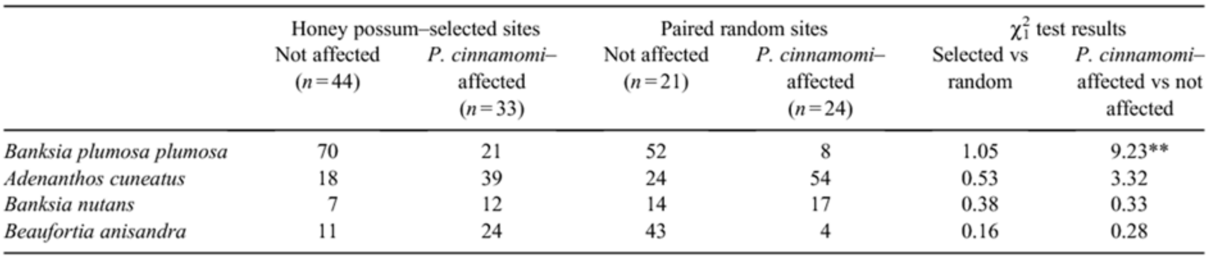
Table 2. Comparison of average (± 1 s.d.) vegetation structure parameters for the four location categories

Asterisks represent significant differences between honey possum–selected and random sites or affected and unaffected sites as determined by factorial ANOVA (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). Letters link groups not significantly different from each other at $P < 0.05$ (each vegetation parameter tested separately and letters on each row only indicate differences between the four categories for that parameter) as determined by Tukey's unequal-*n* HSD tests



	Honey possum–selected sites		Paired random sites		Summary of factorial analyses	
	Not affected ($n=44$)	*P. cinnamomi*–affected ($n=33$)	Not affected ($n=21$)	*P. cinnamomi*–affected ($n=24$)	Selected vs random	*P. cinnamomi*–affected vs not affected
Mean vegetation height (cm)	90.2 ± 23.7^{a}	71.8 ± 26.2^{ac}	77.1 ± 23.9^{ab}	56.3 ± 9.20^{c}	$F_{1,118} = 11.46$***	$F_{1,118} = 21.57$***
% Vegetation coverage	76.4 ± 15.9^{a}	67.6 ± 17.9^{ab}	70.0 ± 19.0^{ab}	58.8 ± 15.4^{b}	$F_{1,118} = 5.68$*	$F_{1,118} = 9.88$**
Number of touches per height class (average across all heights: 0–230 cm)	1.22 ± 0.33^{a}	0.98 ± 0.31^{b}	0.84 ± 0.21^{bc}	0.62 ± 0.19^{c}	$F_{1,118} = 47.56$***	$F_{1,118} = 18.74$***
No. of touches per height class (40–140 cm)	1.77 ± 0.66^{a}	1.17 ± 0.61^{b}	1.01 ± 0.42^{bc}	0.58 ± 0.33^{c}	$F_{1,118} = 41.29$***	$F_{1,118} = 24.83$***
Average of Shannon's Diversity Index (structural complexity)	1.04 ± 0.09^{a}	0.91 ± 0.13^{b}	0.90 ± 0.07^{b}	0.79 ± 0.08^{c}	$F_{1,118} = 54.00$***	$F_{1,118} = 42.70$***

Table 3. Percentage of sites where each of four main food plant species were present
Asterisks represent significant differences between honey possum–selected and random sites or affected and unaffected sites as determined by factorial ANOVA (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$)



	Honey possum–selected sites		Paired random sites		χ^2_1 test results	
	Not affected ($n = 44$)	*P. cinnamomi*–affected ($n = 33$)	Not affected ($n = 21$)	*P. cinnamomi*–affected ($n = 24$)	Selected vs random	*P. cinnamomi*–affected vs not affected
Banksia plumosa plumosa	70	21	52	8	1.05	9.23**
Adenanthos cuneatus	18	39	24	54	0.53	3.32
Banksia nutans	7	12	14	17	0.38	0.33
Beaufortia anisandra	11	24	43	4	0.16	0.28