

Reduced abundance and species richness of forest beetles associated with dieback of kauri (*Agathis australis*) trees due to *Phytophthora agathidicida*

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Abstract: Kauri dieback disease, caused by the soil-borne oomycete pathogen *Phytophthora agathidicida*, has spread through much of New Zealand's kauri (*Agathis australis*) forest, killing thousands of trees. However, whether kauri dieback affects the broader biological community in kauri forests is largely unknown. Here we test whether dieback of kauri trees affected ecologically important beetle communities by sampling beetles using flight-intercept and pitfall traps at three pairs of symptomatic (widespread dieback of kauri trees) and asymptomatic (little or no dieback) forest sites in Waitākere Ranges Regional Park. We collected 4366 individual beetles from 377 species and found that beetle abundance and species richness were significantly lower (34% lower abundance and 19% lower species richness) in symptomatic sites than in asymptomatic sites, whereas beetle diversity and community composition showed no significant differences. The lower abundance and species richness observed in symptomatic sites were consistent across feeding guilds and not just those directly associated with living or dead kauri trees, suggesting that the changes in beetle abundance and richness may be related to environmental changes caused by the loss of dominant canopy trees rather than the loss of kauri trees specifically. Our study presents early evidence that kauri dieback disease may have impacts that extend beyond the host species. As the disease progresses at local and regional scales, long-term monitoring of a broad range of taxa will be required to fully evaluate the impacts of kauri dieback on insect communities, as well as any direct impacts on kauri-specialist species and ecosystem functioning.

Keywords: Coleoptera, community composition, community ecology, disease, diversity, oomycete, plant pathogen, Waitākere Ranges

Introduction

Invasive pests and diseases can severely impact indigenous forest tree species, leading to dieback and death (Loehle et al. 2023). In extreme cases, previously dominant tree species can be extirpated from landscapes (Yan et al. 2005; Haack et al. 2010) or even driven to functional extinction (Griffin 2000; Herms & McCullough 2014). The loss of so many trees can have significant effects on other species in those habitats, leading to changes in species richness and abundance, community composition, and ecosystem services and functioning (Hausman et al. 2010; Sire et al. 2022). In New Zealand, the emergence and spread of plant pathogens such as myrtle rust (*Austropuccinia psidii*) and kauri dieback (*Phytophthora agathidicida*) threatens to reduce populations of susceptible tree species and alter biological communities (Bradshaw et al. 2020).

Kauri (*Agathis australis*) is a dominant emergent canopy tree species that is endemic to northern New Zealand. Mature trees can live for over 1500 years, reach 50 m in height, and have a trunk diameter of up to 4.4 m (Steward & Beveridge

2010), although an age of 600 years and a diameter of 1.5 m is more typical of existing forest (Ahmed & Ogden 1987). At the time of European settlement, kauri forest covered c. 1 million ha of land in the northern North Island, but extensive logging and burning has reduced the amount of old growth kauri forest to less than 1% (7500 ha) of its previous range (Steward & Beveridge 2010). An additional 60 000 ha of regenerating forest and scrubland contains some young kauri trees (Ahmed & Ogden 1987; Steward & Beveridge 2010). Kauri forest typically has a subcanopy of podocarp and broadleaf species, such as rimu (*Dacrydium cupressinum*), rewarewa (*Nightia excelsa*), tawa (*Beilschmiedia tawa*), and tānekaha (*Phyllocladus trichomanoides*), as well as a diverse understory of endemic trees, shrubs, and ferns (Ecroyd 1982; Wyse et al. 2014). The crowns of kauri trees can support diverse communities of epiphytic plants (Bellgard et al. 2016). Although kauri forests support a high biodiversity of indigenous species (Ward et al. 2014), there are no studies we know of that have specifically examined the fauna associated with kauri trees. However, a few insects are known to specialise on kauri trees for their development, such as the kauri leaf

miner, *Acrocercops leucocyma* (Lepidoptera: Gracillariidae) and possibly the small longhorn beetle *Microlamia pygmaea* (Coleoptera: Cerambycidae) (Martin 2000). Kauri is also the only known native host of the wood boring short-nosed kauri weevil, *Xenocnema spinipes* (Coleoptera: Curculionidae), although this species is now common on introduced conifers.

Phytophthora agathidicida is a soil-borne oomycete pathogen that infects the roots of kauri trees, causing kauri dieback disease which is characterised by root and collar rot that prevents the uptake of water and nutrients (Beever et al. 2009). It was first found in the Waitākere Ranges west of Tāmaki Makaurau | Auckland in 2006 (Beever et al. 2009) and was subsequently detected across much of the natural range of kauri in northern New Zealand (Waipara et al. 2013; Bradshaw et al. 2020). Infected trees suffer from resin bleeding, defoliation, and eventual death (Beever et al. 2009; Waipara et al. 2013), although these chronic symptoms are only observed late in the disease progression (Bellgard et al. 2016; Bradshaw et al. 2020). It typically takes 1–10 years from symptom development to mortality (Bradshaw et al. 2020), and trees can be infected for several years before symptoms become obvious (Bellgard et al. 2016). Trees of all ages and sizes are affected, although decline is more rapid for smaller trees (Beever et al. 2009). The main vector for *P. agathidicida* appears to be humans inadvertently moving infected soil on their shoes or other equipment, since most infections occur along walking tracks (Hill & Waipara 2017), although feral pigs (*Sus scrofa*) may also contribute to its spread (Bassett et al. 2017).

The impact of the loss of so many kauri trees on the wider biological community is largely unknown. The death of these trees will have positive to negative impacts on other organisms, both directly (e.g. on species that rely on kauri for food or habitat) and indirectly (e.g. through changes to plant composition, canopy structure, nutrient cycling, abiotic conditions, or species interactions) (Ellison et al. 2005; Thom & Seidl 2016). Short- to medium-term changes may include increased availability of dead wood for xylophagous species, reduced competition for space in the canopy for light-dependent trees, and increased light reaching the forest floor. Over the long-term, the loss of tree species from forests in other parts of the world has resulted in changes to insect community composition and ecosystem functioning (Boyd et al. 2013), including decomposition, nutrient cycling (Silvester 2000), and carbon sequestration (Ellison et al. 2005). For example, the widespread loss of ash (*Fraxinus* spp.) trees in North America following the invasion of emerald ash borer (*Agrilus planipennis*, Buprestidae) has led to widespread changes to understory abiotic conditions, plant community composition, nutrient cycling, successional dynamics, and the availability of woody debris, as well as directly impacting dozens of host-specific insect species (Herms & McCullough 2014). Therefore, the wider impact of kauri dieback disease on forest biodiversity is an important question to address.

Beetles comprise 25% of all animal species on Earth (Farrell 1998; Grove & Stork 2000) and display an almost unparalleled taxonomic and functional diversity (Wardhaugh et al. 2014). For this reason, beetles are frequently used as indicator species for biodiversity assessments of New Zealand invertebrate communities (Hutcheson & Kimberly 1999; Ward & Larivière 2004; Ewers et al. 2007; Pawson et al. 2011; Ward et al. 2014; Wardhaugh & Pawson 2023). In this study, we compared the abundance, species richness, diversity, and composition of beetle communities sampled from paired sites that were symptomatic and asymptomatic for kauri dieback

disease, both overall and for different beetle feeding guilds. Previous studies from other parts of the world have found that large-scale disturbance events that affect natural habitats, such as wide-scale dieback of dominant canopy trees from disease, pest outbreaks, or extreme weather events, often result in reductions to insect abundance or changes to community composition before they impact species richness (Wagner 2020; Cai et al. 2021; Cours et al. 2021; Wagner et al. 2021; Sire et al. 2022). We assume that the loss of many dominant canopy trees in dieback-affected kauri forests has changed abiotic and/or biotic conditions (e.g. open canopy, plant community composition, etc.) at a local scale. We therefore hypothesised that symptomatic sites would have reduced beetle abundance and altered community composition compared to asymptomatic sites, but no differences in species richness and diversity. Furthermore, since beetles are a dominant taxonomic group associated with dead wood (Müller et al. 2010; Lassauce et al. 2011; Sandström et al. 2019; Thorn et al. 2020), we hypothesised that xylophagous species, particularly those known to feed on dead kauri wood, such as *Xenocnema spinipes* and *Mitrastethus baridioides*, would be more abundant in symptomatic sites than in asymptomatic sites due to the greater amount of available dead kauri wood.

Methods

Study site

The study was conducted in Waitākere Ranges Regional Park, west of Tāmaki Makaurau | Auckland (Fig. 1). The park covers approximately 17 000 ha and experiences a subtropical climate (c. 1600 mm annual rainfall, mean annual temperature c. 10 °C) (Chappell 2014). Much of the forest within the park was logged in the past, although some of the more inaccessible areas, such as around Cascades, retain significant areas of old growth kauri forest.

Three pairs of sites (Cascades, Huia, and Piha; Fig. 1; each 40 × 50 m or 2000 m²) that were symptomatic and asymptomatic for kauri dieback disease (six sites total) were established in kauri forest between 2011 and 2015 to study the biological and ecological impacts of kauri dieback in Waitākere Ranges Regional Park. At the time of establishment, all three asymptomatic sites were free of kauri dieback disease. However, *P. agathidicida* has now been detected at the asymptomatic sites at Cascades and Huia. As the infections at these sites are relatively recent, and it takes up to ten years from infection to tree mortality, our study could be more accurately described as a comparison between old symptomatic sites with widespread dieback of kauri trees and newly symptomatic sites with little or no tree mortality to date. For clarity, we refer to all three of the original asymptomatic sites as asymptomatic when making comparisons.

Beetle collection

We focussed on beetles due to their high taxonomic and functional diversity, and because they may be indicator species for changes in the abundance, richness, and composition of broader invertebrate communities (Wardhaugh et al. 2014). Beetles were sampled using flight-intercept traps (FITs) and pitfall traps (Appendix S1 in Supplementary Material). Since both trap types passively collect active insects, samples are best considered a function of true abundance and activity rate. For clarity, we refer to this ‘activity-abundance’ as ‘abundance’

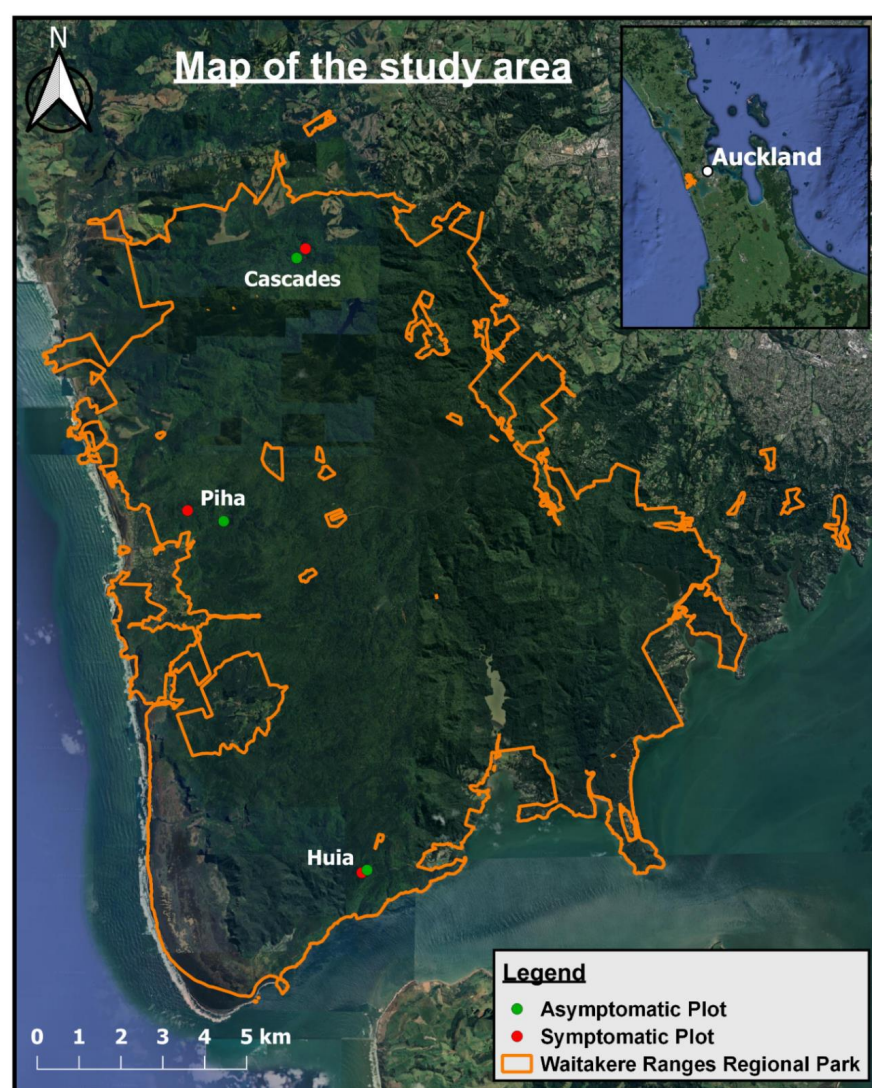


Figure 1. Location of study sites in kauri (*Agathis australis*) forest that were asymptomatic (green) and symptomatic (red) for kauri dieback disease (*Phytophthora agathidicida*) in Waitākere Ranges Regional Park, New Zealand. Figure reproduced with permission from Cordes (2023).

throughout the manuscript. The FITs consisted of two black malflute™ cross-baffles (600 × 210 mm) positioned over a funnel and collection cup approximately half-filled with 100% monopropylene glycol (TMK Packers Ltd., New Zealand), which acted as a killing solution and preservative (Kerr et al. 2022). Each FIT was topped with a large square piece of stiff plastic (400 × 400 mm) to minimise leaves and rain falling into the collection cup. The FITs were attached to metal stakes or small trees at breast height using plastic cable ties. Pitfall traps were plastic cups (75 mm diameter, 100 mm depth) dug into the ground so that the rim of the cup was at or just below ground level, and approximately half-filled with 100% monopropylene glycol. Roofs made from a square of black malflute™ (250 × 250 mm) were suspended c. 50 mm above the traps with two tent pegs to prevent leaves and rain from filling the cups.

Five FITs and five pitfall traps were installed at each site (60 traps total) from 25–27 October 2023 to 5–8 February 2024. Traps of the same type were placed ad hoc within each site, positioned at least 10 m apart. Traps were cleared on four occasions during the study, with sampling periods ranging from 11 to 37 days. A total of 238 samples were collected due to the loss of two samples in the field, one pitfall sample and one from an FIT, both from the asymptomatic site at Huia operating from 25 October to 10 November. All adult

beetles were sorted to species or morphospecies (hereafter referred to as species). Representatives of each species were pinned or pointed to build a reference collection, which is stored at the National Forest Insect Collection (FRNZ) at the Bioeconomy Science Institute, in Rotorua, New Zealand. Specimens that were not dry mounted, as well as non-beetle bycatch, were preserved in 70% ethanol. All beetle species were allocated to a feeding guild based on their known biology or their presumed biology inferred from closely related taxa. These feeding guilds were fungivores (species that feed on fungi), herbivores (species that feed on living plant tissue), predators (species that feed on other invertebrates), scavengers (species that feed on decomposing organic matter), xylophages (species that feed on dead wood), and unknown. The unknown category includes potential omnivorous species and species for which we have no specific information and whose close relatives vary in their feeding guilds, precluding any confident inferences. For our study, these unknowns were all click beetles (Elateridae), which include various predatory, herbivorous, and omnivorous species.

Statistical analyses

Species accumulation curves (SAC) that compare species richness with increasing sample size in symptomatic and asymptomatic sites were built using the “random” method that

finds the mean SAC and its standard deviation from random permutations of sample order (Gotelli & Colwell 2001).

To test whether beetle alpha diversity varied between symptomatic and asymptomatic sites, we used a Linear Mixed Model. Shannon alpha diversity was calculated per sample and used as the response variable, with forest type (asymptomatic forest or symptomatic forest) as the explanatory variable. Trap identity and site were used as random factors to account for non-independence of repeated measures from the same traps and sites. Finally, to adjust for the slightly different numbers of sampling days among traps, we included log-transformed trap days per sample as an offset. For these analyses, each trap was defined as a sampling unit (60 total traps) with four repeated measures each, as every trap was cleared four times.

To compare beetle abundance and species richness between symptomatic and asymptomatic sites, we used Generalised Linear Mixed Models (GLMMs) with negative binomial distributions (*nbinom1* function in R). After model reduction (see below), abundance or species richness per sampling unit were used as the response variable in their respective models, with beetle feeding guild (predator, fungivore, herbivore, scavenger, xylophage, or unknown) and forest type as the explanatory variables. For these comparisons, a negative binomial model is a generalisation of the Poisson model, which relaxes the restrictive assumption that the variance and mean are equal. It differs from a Poisson model (Hilbe 2014) in that it allows a variance higher than the mean (overdispersion) (Yirga et al. 2020). As part of model selection, the full models (considering the interaction) were further reduced with the stepwise method by excluding nonsignificant interactions (Crawley 2010). We again included trap identity and site as random factors and log-transformed trap days per sample as an offset. Post-hoc pairwise comparisons between groups were conducted using estimated marginal means derived from the reduced model. Pairwise contrasts were adjusted for multiple testing using the Sidak correction to control the family-wise error rate (Lenth 2023). Estimated marginal means (or least-squared means) are defined as marginal means of model predictions over a grid comprising all factor combinations, including random factors (Lenth 2023).

To compare the community composition of beetles between symptomatic and asymptomatic sites and between trap types, we used Permutational Multivariate Analysis of Variance (PERMANOVA) and non-metric multidimensional scaling (NMDS) to visualise the data. First, we calculated Bray–Curtis distances between individual samples based on a matrix containing abundance values, with beetle species as columns and samples as rows, using the *avgdist* function. Second, a PERMANOVA test (*adonis2* function) was performed using the Bray–Curtis distance matrix as the response variable, and forest type and trap type as explanatory variables. The groups of data (symptomatic vs. asymptomatic forest and FITs vs. pitfall traps) were also tested for homogeneity of variation with permutation tests using the *betadisper* and *permutest* functions, as this is an assumption for PERMANOVA (Anderson 2017). For visualisation, NMDS scores (*metaMDS* function) were obtained using the Bray–Curtis distance matrix. For a good representation of the data, the stress value of the NMDS should ideally be between 0.1 and 0.2 (Micallef & Schembri 1998). When stress is close to 0 it may indicate the presence of at least one outlier sample. The stress score for our full data set (238 samples) was 0.0004. Consequently, six samples were omitted from the analysis and the resulting NMDS stress of 0.122 indicated sufficient fit.

All analyses were performed in R version 4.2.2 (R Core Team 2022). For the GLMMs, different packages were used: “lme4” (Bates et al. 2015) for running the models, “car” (Fox & Weisberg 2019) to obtain type-III analysis-of-variance tables for the model, and “emmeans” (Lenth 2023) for contrast tests. Shannon alpha diversity indices, species accumulation curves, NMDS, and PERMANOVA were all conducted using the “vegan” package (Oksanen et al. 2022).

Results

We collected a total of 4366 beetles from 377 species and 46 families. Of these, 347 taxa (92%) could be identified to at least the level of genus, while two species (*Leiodinae* n. gen. sp. 1, *Leiodidae*; *Epiphanini* n. gen. sp. 1, *Eucnemidae*) belong to undescribed genera. Sampling effort (trap days) varied little between site pairs (0–2.5% of total trap days) as we lost only two samples, both from the asymptomatic site at Huia. The number of beetles collected per sample varied greatly, ranging from 1 to 91 individuals.

Beetle abundance was 34% higher in asymptomatic (22.2 ± 1.4 individuals per sample, estimated marginal mean ± 1 SEM) than symptomatic sites (14.6 ± 1.2) ($\chi^2_{(1, 1418)} = 8.68$, $P = 0.003$) (Appendix S2). The lack of a significant interaction between forest types and beetle feeding guilds in the model indicated that the difference in beetle abundance did not depend on feeding guild. Beetle abundance differed among feeding guilds ($\chi^2_{(5, 1418)} = 332.26$, $P < 0.0001$), and these results are presented in the Supplementary Materials (Appendices S2 & S3).

A total of 284 and 257 species were collected from asymptomatic and symptomatic sites, respectively (Table 1, Fig. 2). On average, beetle species richness was 19% higher in asymptomatic (9.8 ± 0.5 species per sample) than symptomatic sites (7.9 ± 0.4) ($\chi^2_{(1, 1418)} = 5.13$, $P < 0.023$) (Appendix S4). There was again a lack of a significant interaction between forest types and beetle feeding guilds, indicating that the difference in beetle species richness did not depend on feeding guild. Similarly to abundance, species richness differed among feeding guilds ($\chi^2_{(5, 1418)} = 519.96$, $P < 0.0001$), and these results are presented in the Supplementary Materials (Appendix S4). Shannon alpha diversity per trap ranged from 0.8 to 2.5, with a mean of 1.8 ± 0.1 , but did not differ between symptomatic and asymptomatic sites ($\chi^2_{(1, 233)} = 1.47$, $P = 0.225$) (Table 1).

Although the PERMANOVA indicated that beetle community composition differed between asymptomatic and symptomatic sites ($F_{(1, 229)} = 1.75$, $P = 0.002$), sample variance (i.e. beta diversity) also differed between sites ($F_{(1, 230)} = 6.13$, $P = 0.016$), meaning that the PERMANOVA results have to be taken with caution (Anderson 2001). In addition, visualisation of the NMDS showed substantial overlap between asymptomatic and symptomatic sites (Fig. 3). Lastly, the different trap types collected complementary faunas ($F_{(1, 229)} = 16.04$, $P = 0.001$; Appendix S6).

Discussion

Beetle abundance and species richness were 34% and 19% higher, respectively, in asymptomatic than in symptomatic kauri forest sites (Table 1), suggesting that beetle populations may decline in forest areas suffering from kauri dieback. However, beetle alpha diversity and community composition did not differ

Table 1: The mean (± 1 SEM) alpha diversity, abundance, and species richness of beetles collected at three kauri (*Agathis australis*) forest sites that were asymptomatic and symptomatic for kauri dieback disease (*Phytophthora agathidicida*) in Waitākere Ranges Regional Park, New Zealand. Beetles were collected using pitfall traps and flight-intercept traps. Variables that significantly differed between asymptomatic and symptomatic sites are given in bold.

Variable	Mean $\pm$ SEM per sample		Total	
	Asymptomatic	Symptomatic	Asymptomatic	Symptomatic
Shannon diversity	1.81 (± 0.057)	1.70 (± 0.059)	NA	NA
Abundance	22.2 (± 1.44)	14.6 (± 1.17)	2619	1747
Species richness	9.81 (± 0.515)	7.92 (± 0.446)	284	257

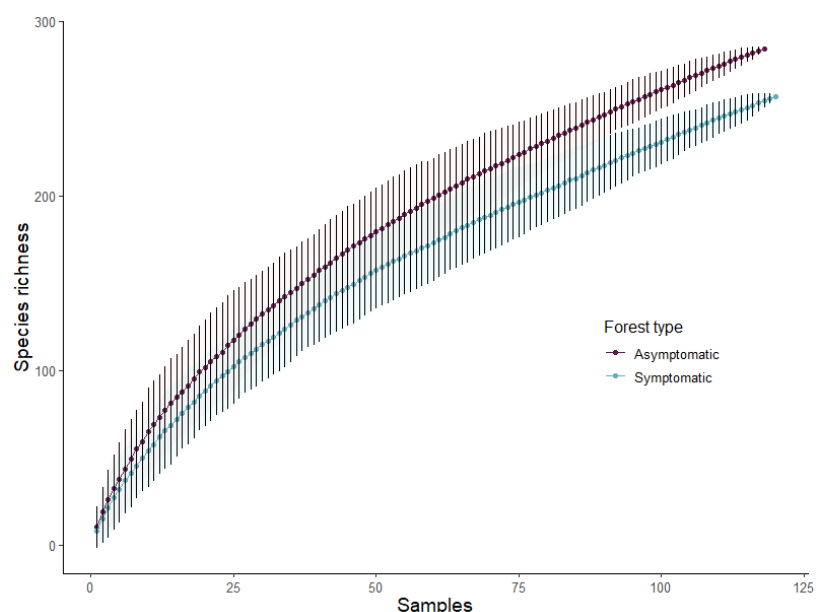


Figure 2. Species accumulation curves of beetles from samples collected using pitfall traps and flight-intercept traps from kauri (*Agathis australis*) forest sites that were asymptomatic (red) and symptomatic (blue) for kauri dieback disease (*Phytophthora agathidicida*) in Waitākere Ranges Regional Park, New Zealand. Curves were built using the “random” method (Gotelli & Colwell 2001), which finds the mean curve and its standard deviation from random permutations of the data. The shaded area represents the 95% confidence interval.

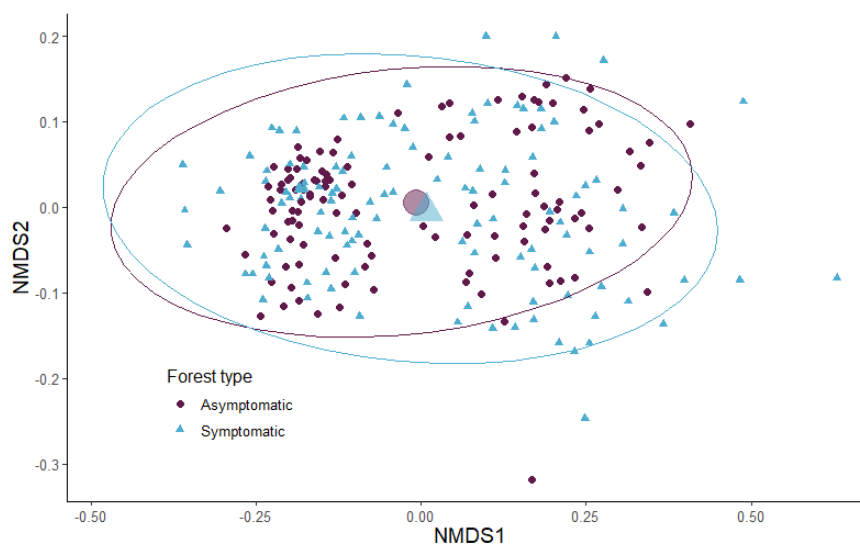


Figure 3. Ordination plot using non-metric multidimensional scaling (NMDS, stress = 0.122) and showing the similarity of beetle communities between kauri (*Agathis australis*) forest sites that were asymptomatic (red) and symptomatic (blue) for kauri dieback disease (*Phytophthora agathidicida*) in Waitākere Ranges Regional Park, New Zealand. Beetles were collected using pitfall traps and flight-intercept traps. Each small point represents a sampling event, and sampling events with similar beetle community composition are closer in the ordination space. The two larger points represent the centroids for beetle communities sampled from asymptomatic and symptomatic kauri forest and ellipses represent 95% confidence intervals around each centroid. Six samples were omitted from the analysis as these were outliers that decreased stress to 0.0004. For a good representation of the data, the stress value should ideally be between 0.1 and 0.2. Permutational Analysis of Variance (PERMANOVA) indicated that beetle community composition differed between asymptomatic and symptomatic kauri forest ($F_{(1, 229)} = 1.75$, $P = 0.002$), but this was not visually supported by the ordination plot.

between symptomatic and asymptomatic sites. These results were consistent with our hypothesis that beetle abundance would decline and diversity would remain unchanged in sites with kauri dieback. However, the decline in species richness and lack of any difference in community composition were not consistent with our hypothesis.

We found no evidence to support our second hypothesis, that xylophagous species known to feed on dead kauri wood, such as *Mitrastethus baridioides* (long-nosed kauri weevil) and *Xenocnema spinipes* (short-nosed kauri weevil), would be more abundant in symptomatic than asymptomatic sites due to the greater amount of available dead kauri wood. Although 46 of the 47 *X. spinipes* individuals collected were from symptomatic sites, 45 were from the Huia site, and 41 from a single trap. This pattern suggests that dead wood near this trap was infested with *X. spinipes* and is not necessarily indicative of a general population increase due to kauri dieback. No *M. baridioides* were collected. The lack of any clear increase in the abundance of these xylophagous species could be due to the state or stage of decay of dead kauri trees within these sites. For example, *M. baridioides* only reproduces in damp or wet wood (Hosking 1978). It is possible that dead wood in the symptomatic sites dries quickly due to increased exposure to sunlight and wind, preventing successful reproduction of *M. baridioides*. Although less is known about the reproductive requirements of *X. spinipes*, it has been shown that they strongly prefer attacking the wood of trees that have been dead for less than one year (A. Sky 2011, University of Canterbury, unpubl. data). Most of the available dead wood at symptomatic sites was from trees that have been dead for several years and may therefore be too decomposed to support this species.

Although our results suggest that beetle abundance and species richness were lower in kauri forests suffering from kauri dieback disease, there is little indication from our data that dieback affected beetle diversity or community composition. Similar results, where one measure of an insect community was impacted by disturbance but not another, have been found in other parts of the world. For example, insect community composition but not species richness was affected by canopy dieback caused by herbivorous insects or drought in European forests (Cai et al. 2021; Cours et al. 2021; Sire et al. 2022). Why one community measure may change for a particular group of insects at a particular site and not another, is not easily explained and may be due to local scale factors, such as rates of dead wood deposition, changes to plant communities, and successional processes (Cours et al. 2021; Sire et al. 2022). In some cases, species that are better adapted to the altered habitat replace those most sensitive to the changes (Sire et al. 2022). This can result in significant changes to community composition without affecting species richness. The decline in species richness we observed suggests that rare species were being lost from areas affected by kauri dieback, while the more common species that compose the core of the beetle community remain, though often at lower abundances. This would be consistent with our result that community composition remained unchanged between symptomatic and asymptomatic sites, since the majority of species were still present.

There are several possible explanations for why kauri dieback could result in reduced abundance and species richness of beetles but have little to no impact on their diversity or community composition. First, the consistent effect across multiple feeding guilds suggests that abundances and species richness are being affected by changes to abiotic conditions, such as temperature and humidity, rather than the loss of a

single tree species (Sire et al. 2022). For example, increased temperature and reduced humidity could negatively impact forest-adapted beetle species by increasing their rates of water loss. Alternatively, changes in abiotic conditions associated with kauri dieback may affect the resources on which some of these beetles rely. For example, canopy dieback following attack by the bark beetle *Ips typographus* (Curculionidae: Scolytinae) was found to greatly reduce fungal biomass and alter fungal community composition in the litter and soil of a spruce (*Picea abies*) forest in Central Europe (Štursová et al. 2014). A reduction in resources, such as foliage, fungi, or insect prey, could decrease the abundance of associated beetles. However, changes in community composition and diversity may not occur until resources are more depleted or lost over large spatial scales. Therefore, the lack of an effect on diversity or community composition may be because kauri dieback is not yet severe or widespread enough to result in larger-scale changes to beetle communities. A further consideration is that there may be a time lag between the loss of kauri trees and the full impacts on the local beetle fauna, which may not be realised for many years.

The lack of differences in community composition between symptomatic and asymptomatic sites may be at least partly explained by the evolutionary history and unique composition of the New Zealand flora and fauna. The New Zealand beetle fauna is largely a fauna of the forest (Klimaszewski & Watt 1997), and most species are therefore expected to be adapted to the cool, damp, and shady abiotic conditions prevalent in closed canopy, old growth forest. The loss of canopy trees allows more light and wind to penetrate to the forest floor, leading to warmer, drier, and lighter conditions (Kopáček et al. 2020) that are assumed to be suboptimal for most New Zealand beetle species. However, the paucity of endemic beetle species adapted to more open environments (Klimaszewski & Watt 1997), particularly in lowland areas of the North Island, may help to explain why community composition did not change after dieback. Studies from Europe often find changes to insect community composition because open habitat species move into forest areas after a disturbance (Cai et al. 2021; Cours et al. 2021; Sire et al. 2022). In our study, it seems that the existing forest community simply decreased in abundance and species richness with the loss of canopy trees, rather than being replaced by species better adapted to the disturbed environment. We cannot, however, discount the limitations of our study, where we had relatively few sites and our sampling was restricted to a single summer. Sampling a wider range of sites and over a longer period will help to more fully resolve the impacts of kauri dieback on beetle communities.

Although we found no evidence for kauri dieback impacting beetle diversity or community composition, the loss of kauri trees was associated with lower beetle abundance and species richness. This result was observed across feeding guilds, suggesting that the decreased beetle abundance and species richness may be related to altered environmental conditions from the loss of canopy trees (e.g. increased light and wind, and reduced humidity), rather than to the loss of kauri trees specifically. Reduced abundance of insects is a common early impact from large-scale disturbance events, such as forest dieback from disease or pest outbreaks (Wagner 2020; Wagner et al. 2021). It should be noted that kauri dieback has thus far affected a relatively small area of kauri forest in the Waitākere Ranges, and for a relatively short amount of time. As the disease progresses at local and regional scales, long-term monitoring will be needed across more affected

areas, and will need to incorporate more taxa and measures of ecosystem functioning to fully understand the community and ecosystem-wide impacts of kauri dieback disease.

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Additional information and declarations

Author contributions: CW conceived and designed the sampling program and wrote the first draft of the manuscript. CW and HB carried out field and laboratory work. SA carried out the statistical analyses. All authors contributed to the writing of the manuscript.

Data and code availability: The datasets presented in this article are not readily available because the data in this research were collected from the traditional lands of Te Kawerau ā Maki with their permission. The authors recognise their sovereignty and authority to control data about their lands under the CARE Principles for Indigenous Data Governance. Requests to access the datasets should be directed to l.schwendenmann@auckland.ac.nz.

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Conflict of interest: The authors declare no conflicts of interest.

References

- Ahmed M, Ogden J 1987. Population dynamics of the emergent conifer *Agathis australis* (D. Don) Lindl. (kauri) in New Zealand I. Population structures and tree growth rates in mature stands. *New Zealand Journal of Botany* 25: 217–229.
- Anderson MJ 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32–46.
- Anderson MJ 2017. Permutational multivariate analysis of variance (PERMANOVA). In: Balakrishnan N, Colton T, Everitt B, Piegorsch W, Ruggeri F, Teugels JL eds. *Wiley StatsRef: Statistics Reference Online*. John Wiley & Sons, Ltd. Pp.1–15.
- Bassett IE, Horner IJ, Hough EG, Wolber FM, Egeter B, Stanley MC, Krull CR 2017. Ingestion of infected roots by feral pigs provides a minor vector pathway for kauri dieback disease *Phytophthora agathidicida*. *Forestry* 90: 640–648.
- Bates D, Mächler M, Bolker B, Walker S 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67(1): v067.i01.
- Beever RE, Waipara NW, Ramsfield TD, Dick MA, Horner IJ 2009. Kauri (*Agathis australis*) under threat from *Phytophthora*? *Phytophthoras in forests and natural ecosystems*. Proceedings of the Fourth Meeting of the International Union of Forest Research Organizations Working Party S07.02.09. Pp 74–85.
- Bellgard SE, Pennycook SR, Weir BS, Ho W, Waipara NW 2016. *Phytophthora agathidicida*. *Forest Phytophthoras* 6(1): 3719.
- Boyd IL, Freer-Smith PH, Gilligan CA, Godfray HCJ 2013. The consequences of tree pests and diseases for ecosystem services. *Science* 342: 1235773.
- Bradshaw RE, Bellgard SE, Black A, Burns BR, Gerth ML, McDougal RL, Scott PM, Waipara NW, Weir BS, Williams NM, Winkworth RC, Ashcroft T, Bradley EL, Dijkwel PP, Guo Y, Lacey RF, Mesarich CH, Panda P, Horner IJ 2020. *Phytophthora agathidicida*: research progress, cultural perspectives and knowledge gaps in the control and management of kauri dieback in New Zealand. *Plant Pathology* 69: 3–16.
- Cai W, Yang C, Wang X, Wu C, Larrieu L, Lopez-Vaamonde C, Wen Q, Yu DW 2021. The ecological impact of pest-induced tree dieback on insect biodiversity in Yunnan pine plantations, China. *Forest Ecology and Management* 491: 119173.
- Chappell PR 2014. The climate and weather of Auckland. NIWA Science and Technology Series, 60. National Institute of Water and Atmospheric Research. 40 p.
- Cordes M 2023. Assessment of forest structural complexity in kauri (*Agathis australis*) dominated stands affected by kauri dieback using mobile terrestrial laser scanning. Unpublished MSc thesis, Georg-August-University, Göttingen, Germany.
- Cours J, Larrieu L, Lopez-Vaamonde C, Müller J, Parmain G, Thorn S, Bouget C 2021. Contrasting responses of habitat conditions and insect biodiversity to pest- or climate-induced dieback in coniferous mountain forests. *Forest Ecology and Management* 482: 118811.
- Crawley MJ 2010. *The R Book*. 2010. The R Book. West Sussex, John Wiley & Sons, Ltd. 975 p.
- Ecroyd CE 1982. Biological flora of New Zealand 8. *Agathis australis* (D. Don) Lindl. (Araucariaceae) Kauri. *New Zealand Journal of Botany* 20: 17–36.
- Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliot K, Ford CR, Foster DR, Kloeppel BD, Knoepp JD, Lovett GM, Mohan J, Orwig DA, Rodenhouse NL, Sobczak WV, Stinson KA, Stone JK, Swan CM, Thompson J, Von Holle B, Webster JR 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3: 479–486.
- Ewers RM, Thorpe S, Didham RK 2007 Synergistic interactions between edge and area effects in a heavily fragmented landscape. *Ecology* 88: 96–106.
- Farrell BD 1998. “Inordinate fondness” explained: Why are there so many beetles? *Science* 281: 555–559.
- Fox J, Weisberg S 2019. An R companion to applied regression. <https://www.john-fox.ca/Companion/> (accessed 20 March 2024).

- Gotelli NJ, Colwell RK 2001. Quantifying biodiversity: procedures and pitfalls in measurement and comparison of species richness. *Ecology Letters* 4: 379–391.
- Griffin GJ 2000. Blight control and restoration of the American chestnut. *Journal of Forestry* 98: 22–27.
- Grove SJ, Stork NE 2000. An inordinate fondness for beetles. *Invertebrate Taxonomy* 14: 733–739.
- Haack RA, Hérard F, Sun J, Turgeon JJ 2010. Managing invasive populations of Asian longhorned beetle and citrus longhorned beetle: A worldwide perspective. *Annual Review of Entomology* 55: 521–546.
- Hausman CE, Jaeger JF, Rocha OJ 2010. Impacts of the emerald ash borer (EAB) eradication and tree mortality: potential for a secondary spread of invasive plant species. *Biological Invasions* 12: 2013–2023.
- Herms DA, McCullough DG 2014. Emerald ash borer invasion of North America: History, biology, ecology, impacts, and management. *Annual Review of Entomology* 59: 13–30.
- Hilbe JM 2014. Modeling count data. Cambridge, Cambridge University Press. 283 p.
- Hill L, Waipara NW 2017. Kauri dieback report 2017: An investigation into the distribution of kauri dieback, and implications for its future management, within the Waitakere Ranges Regional Park. Version 2. Auckland, Auckland Council. 39 p.
- Hosking GP 1978. Longnosed kauri weevil, *Mitrastethus baridioides*. *Forest and Timber Insects in New Zealand* No. 34. Wellington, Government Printer. 4 p.
- Hutcheson JA, Kimberley MO 1999. A pragmatic approach to characterising insect communities in New Zealand: Malaise trapped beetles. *New Zealand Journal of Ecology* 23: 69–79.
- Kerr JL, Dickson G, O'Connor BC, Somchit C, Sweeney J, Pawson SM 2022. Effect of host volatile release rate and racemic fuscumol on trap catch of *Hylurgus ligniperda*, *Hylastes ater* (Coleoptera: Curculionidae), and *Arhopalus ferus* (Coleoptera: Cerambycidae). *Journal of Economic Entomology* 115: 168–177.
- Klimaszewski J, Watt JC 1997. Coleoptera: Family-group review and keys to identification. *Fauna of New Zealand*, number 37. Lincoln, Manaaki Whenua Press. 199 p.
- Kopáček J, Bače R, Hejzlar J, Kaňa J, Kučera T, Matějka K, Porcal P, Turek J 2020. Changes in microclimate and hydrology in an unmanaged mountain forest catchment after insect-induced tree dieback. *Science of the Total Environment* 720: 137518.
- Lassauce A, Paillet Y, Jactel H, Bouget C 2011. Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecological Indicators* 11: 1027–1039.
- Lenth R 2023. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.8.8. <https://CRAN.R-project.org/package=emmeans> (accessed 20 March 2024).
- Loehle C, Hulcr J, Smith JA, Munro HL, Fox T 2023. Preventing the perfect storm of forest mortality in the United States caused by invasive species. *Journal of Forestry* 121(1): 104–117.
- Martin NA 2000. A longhorn leaf miner, *Microlamia pygmaea* (Coleoptera: Cerambycidae: Lamiinae) found in New Zealand. *New Zealand Entomologist* 23: 86.
- Micallef RM, Schembri PJ 1998. The application of multivariate analytical techniques to the study of marine benthic assemblages: a review with special reference to the Maltese Islands. *Xjenza* 3: 9–28.
- Müller J, Noss RF, Bussler H, Brandl R 2010. Learning from a “benign neglect strategy” in a national park: Response of saproxylic beetles to dead wood accumulation. *Biological Conservation* 143: 2559–2569.
- Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, Fitz, JR, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J 2022. ‘vegan’: Community Ecology Package. R package version 2.6-4, <https://CRAN.R-project.org/package=vegan> (accessed 20 March 2024).
- Pawson SM, Brockerhoff EG, Watt MS, Didham RK 2011. Maximising biodiversity in plantation forests: Insights from long-term changes in clearfell-sensitive beetles in a *Pinus radiata* plantation. *Biological Conservation* 144: 2842–2850.
- R Core Team 2022. R: a language and environment for statistical computing. Version 4.2.2. Vienna, Austria, R Foundation for statistical computing. <http://www.R-project.org/>.
- Sandström J, Bernes C, Junninen K, Löhmus A, Macdonald E, Müller J, Gunnar Jonsson B 2019. Impacts of dead wood manipulation on the biodiversity of temperate and boreal forests. A systematic review. *Journal of Applied Ecology* 56: 1770–1781.
- Silvester WB 2000. The biology of kauri (*Agathis australis*) in New Zealand II. Nitrogen cycling in four kauri forest remnants. *New Zealand Journal of Botany* 38: 205–220.
- Sire L, Schmidt Yáñez P, Wang C, Bézier A, Courtial B, Cours J, Fontaneto D, Larrieu L, Bouget C, Thorn S, Müller J, Yu DW, Monaghan MT, Herniou EA, Lopez-Vaamonde C 2022. Climate-induced forest dieback drives compositional changes in insect communities that are more pronounced for rare species. *Communications Biology* 5: 57.
- Steward GA, Beveridge AE 2010. A review of New Zealand kauri (*Agathis australis* (D. Don) Lindl.): its ecology, history, growth and potential for management for timber. *New Zealand Journal of Forestry Science* 40: 33–59.
- Štursová M, Šnajdr J, Cajthaml T, Bárta J, Šantrůčková H, Baldrian P 2014. When the forest dies: the response of forest soil fungi to a bark beetle-induced tree dieback. *The ISME Journal* 8: 1920–1931.
- Thom D, Seidl R 2016. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biological Reviews* 91: 760–781.
- Thorn S, Seibold S, Leverkus AB, Michler T, Müller J, Noss RF, Stork N, Vogel S, Lindenmayer DB 2020. The living dead: acknowledging life after tree death to stop forest degradation. *Frontiers in Ecology and the Environment* 18: 505–512.
- Wagner DL 2020. Insect declines in the Anthropocene. *Annual Review of Entomology* 65: 457–480.
- Wagner DL, Grames EM, Forister ML, Berenbaum MR, Stopak D 2021. Insect decline in the Anthropocene: Death by a thousand cuts. *Proceedings of the National Academy of Science* 118(2): e2023989118.
- Waipara NW, Hill S, Hill LMW, Hough EG, Horner IJ 2013. Surveillance methods to determine tree health, distribution of kauri dieback disease and associated pathogens. *New Zealand Plant Protection* 66: 235–241.

- Ward DF, Larivière MC 2004. Terrestrial invertebrate surveys and rapid biodiversity assessment in New Zealand: lessons from Australia. *New Zealand Journal of Ecology* 28: 151–159.
- Ward DF, Young M, Booth KAM, Beggs JR 2014. Patterns of beetle diversity in kauri forest. *New Zealand Entomologist* 37: 75–82.
- Wardhaugh CW, Pawson SM 2023. Multi-trap sampling of arthropod communities at ports of first entry informs biosecurity surveillance programs. *Journal of Pest Science* 97: 1369–1379.
- Wardhaugh CW, Stork NE, Edwards W 2014. Canopy invertebrate community composition on rainforest trees: different microhabitats support very different invertebrate communities. *Austral Ecology* 39: 367–377.
- Wyse SV, Burns BR, Wright SD 2014. Distinctive vegetation communities are associated with the long-lived conifer *Agathis australis* (New Zealand kauri, Araucariaceae) in New Zealand rainforests. *Austral Ecology* 39: 388–400.
- Yan Z, Sun J, Don O, Zhang Z 2005. The red turpentine beetle, *Dendroctonus valens* LeConte (Scolytidae): an exotic invasive pest of pine in China. *Biodiversity and Conservation* 14: 1735–1760.
- Yirga AA, Melesse SF, Mwambi HG, Ayele DG 2020. Negative binomial mixed models for analyzing longitudinal CD4 count data. *Scientific Reports* 10: 16742.

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Supplementary Material

Additional supporting information may be found in the online version of this article.

Appendix S1. Insect traps.

Appendix S2. Beetle abundances in symptomatic and asymptomatic kauri forest.

Appendix S3. Abundance comparisons among beetle feeding guilds.

Appendix S4. Beetle species richness in symptomatic and asymptomatic kauri forest.

Appendix S5. Species richness comparisons among beetle feeding guilds.

Appendix S6. Similarity of beetle communities between samples collected using different trap types.

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