NEW ZEALAND JOURNAL OF ECOLOGY

RESEARCH

Effect of plant composition on epigeal spider communities in northern New Zealand forest remnants

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Abstract: Te Paki Ecological District (TPED) in northern Northland, New Zealand, is well known as an ecologically significant centre of endemism. However, due to extensive anthropogenic habitat degradation, native forest has been reduced to small, isolated remnants and many of its endemic species are threatened with extinction. Epigeal spider communities (species living on or near the ground) were surveyed within TPED by pitfall trapping at seven native forest remnants differing in plant composition and apparent seral stage to investigate how spider communities varied within them. Surveys were conducted four times over a 12-month period coinciding with winter, spring, summer and autumn. Changes in spider communities were related to differences in plant composition, which were in turn associated with differences in apparent seral stage of the vegetation. Spider communities in forests at later seral stages were dominated by species such as *Rinawa* sp., *Porrhothele* sp. and *Uliodon* sp., whereas *Euryopis nana*, *Cambridgea reinga*, *Stanwellia hollowayi* and *Hypodrassodes apicus* were most prevalent in remnants at earlier seral stages. These species could potentially serve as useful bioindicators of ecological succession or restoration. Apart from soil organic matter content none of the predictor variables tested, including plant species richness, were significantly correlated with spider richness or diversity. Spider richness and diversity are most likely determined by a complex interaction of environmental and temporal factors that operate at different spatial scales. This study has increased our understanding of the ecological associations of spider communities and established that TPED is an important centre of endemism for spiders in New Zealand. We have also demonstrated the importance of forest remnants as reservoirs of indigenous spider diversity and helped resolve several historical taxonomic issues. Furthermore, we demonstrate the need for taxonomic research in this region of New Zealand and highlight the value of such biodiversity surveys.

Keywords: endemism, ground-dwelling, habitat destruction, pitfall trapping, species diversity, Te Paki

Introduction

Spiders (Arachnida: Araneae) are one of the most diverse and abundant groups of large predatory invertebrates in terrestrial ecosystems (Wise 1993). An appreciation of the factors that influence their distribution, and the structure of their communities, is therefore important for understanding food webs and community processes in general. The fact that spiders respond to changing environmental conditions means they can also be used as indicators of various habitat characteristics, including seral stage (Wise 1993; Willett 2001; Gerlach et al. 2013). Spiders have been included in some studies of biodiversity in indigenous ecosystems in New Zealand (Berndt 1998; Alley et al. 2001; Derraik et al. 2001; Sinclair et al. 2005; Michel et al. 2008; Affeld et al. 2009; Lamont et al. 2017), though few of the studies have investigated detailed

environmental predictors of those communities (but see Hodge et al. 2007; Malumbres-Olarte et al. 2013a, 2013b).

Te Paki Ecological District (hereafter TPED) in northern Northland, New Zealand has long been recognised as an area of high biodiversity value. Relative to the size of the area, levels of endemism in plants (Cameron & Jones 1996), lizards (Chapple et al. 2008), molluscs (Goulstone et al. 1993; Marshall & Barker 2007), beetles (Larochelle & Larivière 2005), landhoppers (Duncan 1994; Ball et al. 2017) and other invertebrate groups (Winterbourn 2009; Hoare 2010; Buckley & Bradler 2010) are high. This is most likely due to the geological history of the area, which has experienced prolonged periods of isolation from the mainland during the Pliocene and Pleistocene epochs (Fleming 1979; Balance & Williams 1982). Moreover, many of the endemic species are threatened with extinction due to extensive human-induced

habitat degradation (Lux et al. 2009). In particular, native forest cover has been greatly reduced, leaving only small, isolated remnants. Thus, there is an urgent need for further research into the fauna and flora of TPED. This includes the spiders, for which, to our knowledge, there have been no large-scale ecological or even taxonomic studies conducted within TPED. In fact, if it were not for the collections of BA Holloway, RR Forster, and KAJ Wise in December 1960, January 1967, and February 1967 respectively, little would be known about the TPED spider fauna.

Between 2006 and 2009, large-scale pitfall trapping surveys were conducted in TPED to investigate the ecology of the carabid beetle *Mecodema tenaki* (Ball et al. 2013), and this provided an opportunity to survey other invertebrate taxa. In this paper, we investigate the composition, diversity, and environmental correlates of spider communities in a range of native forest remnants with differing vegetation at different seral stages. We predicted that spider communities would vary depending upon the composition and estimated seral stage of the plant communities. Based on the review by Uetz (1991), we also predicted that spider richness and diversity would be related to plant composition and highest in remnants likely to be at later seral stages. Further, we assessed the significance of TPED and its forest remnants as reservoirs of indigenous spider diversity and evaluated how important such faunal studies are from taxonomic, ecological and conservation perspectives.

Methods

Study area and site selection

The study was conducted in remnants of predominantly native forest in TPED at the northern extremity of New Zealand's North Island (Fig. 1). Seven study sites were randomly selected within certain constraints. All sites needed to be accessible, but also fall within forest habitat. We used Protected Natural Areas Programme (PNAP) survey data (Lux et al. 2009) to define the extent of forest habitat for random site selection, with forest fragments chosen to maximise the geographic range of the sampling across the district. Also, we selected sites with a range of vegetation types, including a variety of putative seral stages. The seral stage can only be estimated since the nature of the vegetation growing at a given site will be determined by numerous environmental factors as well as the previous disturbance regime. The dominant vegetation at Shenstone Block consisted of a mix of kānuka (*Kunzea* sp.), māhoe (*Melicytus ramiflorus*), hangehange (*Geniostoma ligustrifolium*), and red matipo (*Myrsine australis*). The site was located on a foot-slope and was likely at an early seral stage for native forest. The North Cape site, situated near the base of a shallow, moderately sloping gully, also appeared to be at an early stage of succession and was heavily dominated by kānuka and hangehange. Kānuka and hangehange in addition to māhoe also dominated Tapotupotu (B), which was located on a river terrace. Although still probably at an early seral stage, a developing understorey of broadleaved species such as kohekohe (*Didymocheton spectabilis*) and houhere (*Hoheria populnea*) suggests that succession at this site was slightly more advanced. Succession at Te Huka (B), situated on a steep back-slope or face, was probably more advanced still, with species such as nīkau (*Rhopalostylis sapida*) and houhere beginning to dominate under a taller canopy of scattered kānuka. Broadleaved species such as pūriri (*Vitex lucens*), kohekohe, and taraire (*Beilschmiedia tarairi*), characteristic of later seral stages, were also more prominent in the understorey at this site. The vegetation at Tapotupotu (A), also situated on a steep back-slope or face, was dominated by a tall canopy of kohekohe with scattered kōwhai (*Sophora* sp.) and other broadleaved species, indicating a later seral stage. Of all the sites, Haupatoto and Kohuroa (B), both located near the base of large gullies, appeared to be at the latest seral stages, being dominated by taraire, pūriri, karaka (*Corynocarpus laevigatus*),
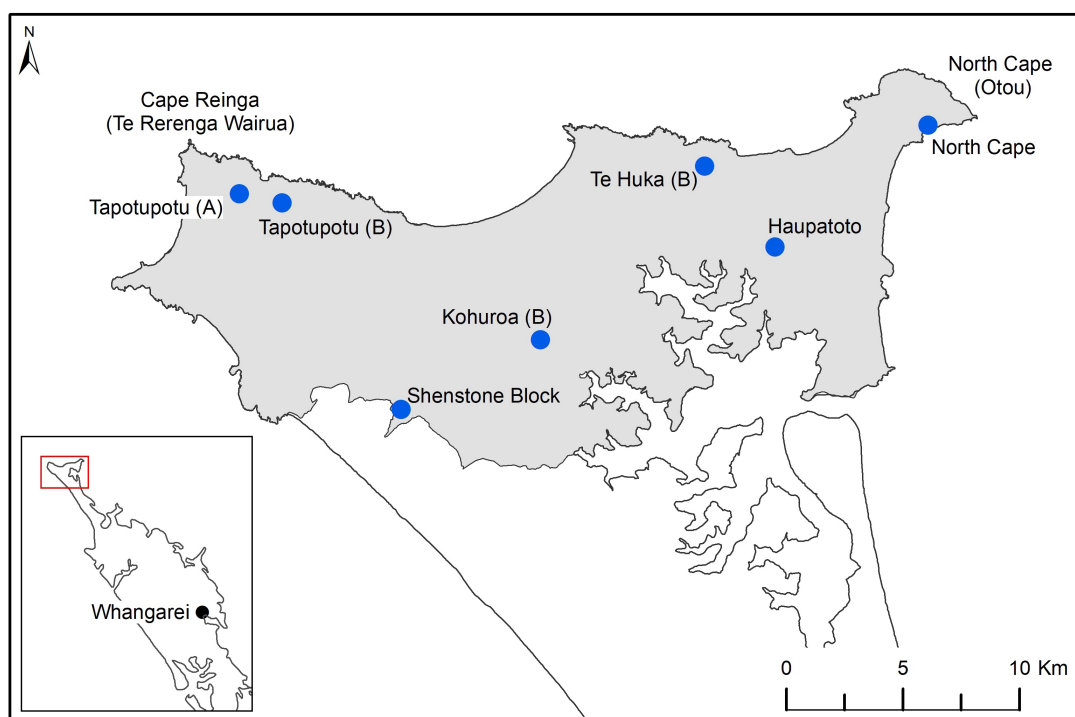

Figure 1. Map of Te Paki Ecological District (grey area) showing locations of the seven study sites.

kohekohe, and nīkau. Further details of site characteristics including ground covers, physical attributes and soil chemistry are presented in Appendix S1 in Supplementary Materials. Precise global positioning system locations of the seven sites are listed in Ball et al. (2013).

Spider sampling

Details of the invertebrate trapping have been described elsewhere (Ball et al. 2013), so only a summary is given here. At each study site, eight plastic pitfall traps (10 cm diameter) were installed level with the ground surface in two rows of four. Traps were placed 10 m apart. Each trap contained approximately 100 ml of the preservative propylene glycol (100%) and was protected by a raised (30 mm) wooden rain cover. Sampling was conducted on four occasions, each lasting four weeks and coinciding with winter (July–August 2008), spring (October–November 2008), summer (January–February 2009), and autumn (April–May 2009). Between each deployment, the traps were closed using securely fitting plastic lids. In the field, the contents of each trap were rinsed in 80% ethanol to remove the preservative and stored in fresh 80% ethanol. In the laboratory, spiders were separated from other invertebrates, identified to the lowest taxonomic level consistent with current names in the World Spider Catalog (2022), counted, and assigned, where possible, to sex and age classes. All spiders are deposited in the Museum of New Zealand Te Papa Tongarewa (MNZ).

Environmental measurements

Data on potential biotic and abiotic predictors of spider communities were collected from each site. The diversity and cover of higher plants (Tracheophyta) within a 30 m diameter plot centred on each trap cluster was assessed using the Reconnaissance (Recce) method (Allen 1992). Importance values were calculated for each plant species by converting cover scores to the mid-point of the percentage cover range associated with each score and summing across tiers (Wiser et al. 2011). Other site attributes recorded were the percent cover of herbaceous vegetation (under 30 cm), moss, rock, bare mineral soil and leaf litter, as well as mean top height of the vegetation, ground slope and leaf litter depth. Soil samples were collected and tested for potassium, calcium, magnesium, sodium, available nitrogen, organic matter content and pH by Hill Laboratories, Hamilton, New Zealand. Further details of the environmental measurements are covered in Ball et al. (2013).

Data analysis

Pitfall trapping provides an effective means of sampling many of the spiders from the ground vegetation and litter; these can be classed as epigeal spiders. However, when samples in a study contain only a singleton or doubleton it is uncertain if the species is epigeal or represents an individual straying from its usual niche. Singletons and doubletons in this study were considered epigeal if they, or their close relatives, were well-represented in litter in surveys undertaken previously in New Zealand. Based on this knowledge, individuals from four species were not considered part of the epigeal spider fauna in this study and were excluded from the analyses. They were *Migas* sp., *Hinewaia* sp., *Ariadna* sp., and an undescribed species of salticid.

All lycosid spiderlings present as a result of a female carrying multiple young falling into a trap were also excluded, as their counts were clearly not a function of random movements of independent individuals.

For analyses investigating differences between adult and juvenile stages, mature males and females of each species were combined into an 'adult' category, and penultimate males (males that will become sexually mature with their next and final moult), immatures and spiderlings were combined as 'juveniles'. Adult and juvenile spiders were combined for all other analyses. However, it was necessary to combine juvenile *Hypodrassodes apicus* and *H. maoricus* as it was not possible to distinguish between them. Therefore, all juvenile *Hypodrassodes* spp. were excluded in the species-level analyses.

Spider abundance and diversity

To examine the effect of season on the overall abundances of adult and juvenile spiders separately, repeated measures ANOVAs were conducted on normally distributed (Shapiro–Wilk test) raw data with associated Tukey's post-hoc tests using the statistical software PAST v3.20 (Hammer et al. 2001). The total species richness recorded across the seven sites (gamma diversity, γ), and the species richness at each site (alpha diversity, α), were determined. To evaluate the taxonomic comprehensiveness of the sampling programme, a sample-based rarefaction curve using sites as replicates was generated with 100 random draws (seasons combined). A sample-based approach was considered most appropriate as this accounts for natural sample heterogeneity (Gotelli & Colwell 2001). Also, Chao-2 and ICE (incidence-based coverage estimator) estimators of species richness were then calculated for each site, as well as for all sites combined. Rarefaction curves and species richness estimates were generated using the software EstimateS v. 9 (Colwell 2013). In addition, we calculated two measures of species diversity for each site, the Simpson Index of Diversity (1 - *D*) and the Shannon–Weiner Species Diversity Index (*H'*) using PAST v3.20 (Hammer et al. 2001). A rank–abundance (Whittaker) plot using relative abundance data was created to view the species richness and abundance distribution at all sites combined.

Spider communities and environmental correlates

Principal coordinates analysis (PCoA) was used to ordinate the study sites in spider species space. Species count data were transformed ($\log_{10} (x + 1)$) to reduce the influence of outliers. Species present at only one site were removed to reduce their disproportionate influence on communities. The response matrix therefore comprised 27 of the 42 spider species recorded across the seven sites. The ordination was based on the Sørensen (Bray–Curtis) distance measure. A joint plot was used to display which spiders contributed most strongly to the gradients reflected by each ordination axis. A second joint plot was used to visualise the correlative associations between ordination scores of the sites in spider space and the measured environmental variables (plant importance values, biotic, and abiotic site attributes and soil chemistry data).

A separate PCoA (also based on the Sørensen distance measure) was used to examine differences in the seven sites based on their plant communities. Plant importance values were transformed ($\log_{10} (x + 1)$) and species present at only one site were removed. The response matrix comprised 65 of the 84 plant species recorded across the seven sites. A joint plot was used to display correlations between plant species and the ordination axes.

A Mantel test was used to determine whether spider communities at the sites were spatially autocorrelated. The Sørensen distance measure was used for the spider data, and

the Euclidean distance measure was used for the locality data (easting and northing coordinates). A second Mantel test was used to examine the similarity of redundancy patterns between spider community and plant community distance matrices (both utilising Sørensen distance). A Monte Carlo test with 1000 randomised runs was used to test the significance of the association in both cases.

The relationships between spider species richness with most of the measured biotic and abiotic predictor variables (plant species richness, percentage ground cover of vegetation, leaf litter, bare soil, mean top height of vegetation, leaf litter depth, and soil chemistry variables) and the axis coordinates of the PCoA in spider space were tested with the Kendall tau (τ) correlation coefficient.

Multivariate analyses were performed using the statistical software PC-ORD v6.22 (McCune & Mefford 2011) and correlations were performed in PAST v3.20 (Hammer et al. 2001).

Results

Spider abundance and diversity

A total of 1617 spiders (628 adults and 989 juveniles) were collected from the seven sites over the four seasons (Appendix S2). Season had a significant effect on overall numbers of adult and juvenile spiders trapped (Fig. 2). Significantly more spiders were trapped in summer than in winter (for adults $P < 0.01$ and for juveniles $P < 0.001$). Numbers of juvenile spiders were also significantly higher in summer than autumn, but not for the adult stage.

Nine hundred and ninety one of the 1617 individuals (61%) were identified to species-specific taxa. Spiders in 42 species, 36 genera, and 18 families were recorded (Appendix S2). Observed species richness at the seven study sites varied from 13–22 species and included eight singletons (19%) and five doubletons (12%) overall (Table 1). The sample-based rarefaction curve for all sites combined (Fig. 3) had not reached an asymptote indicating that the species inventory was not complete. Chao-2 and ICE estimated that an additional 11–15 species were not detected during sampling (Table 1). The species richness estimators for individual sites indicated that the inventories for Tapotupotu (A), Shenstone Block, Haupatoto, and North Cape were close to complete, whereas an estimated 4–12 species remained undetected at the other three sites. The inventory at Tapotupotu (B) was assessed as being particularly incomplete even though it was the most species rich. The Simpson and Shannon–Weiner indices were highly correlated and indicated that the most diverse sites were Tapotupotu (A) and (B) as well as North Cape, whereas the least diverse sites were Te Huka (B) and Haupatoto (Table 1).

The rank–abundance distribution of spiders (all sites combined) indicated that the fauna was dominated by a few very common species (Fig. 4). The five most commonly trapped species, *Rinawa* sp., *Uliodon* sp., *H. apicus*, *Australomimetus* sp., and *Stanwellia hollowayi*, accounted for 60% of the total spider catch identifiable to species. Conversely, most species were trapped in low or very low numbers.

Spider communities and environmental correlates

The PCoA ordination of spider communities generated two axes that explained 72% of the variation in the input data (Fig. 5). The ordination captured signs of both gradients and divisions in spider communities. Spider communities at Shenstone Block and North Cape on the left side of the plot were particularly different to those at the other sites, and Kohuroa (B), Te Huka (B), and Haupatoto formed a loose cluster on the right side of the plot. The two Tapotupotu sites formed another loose cluster
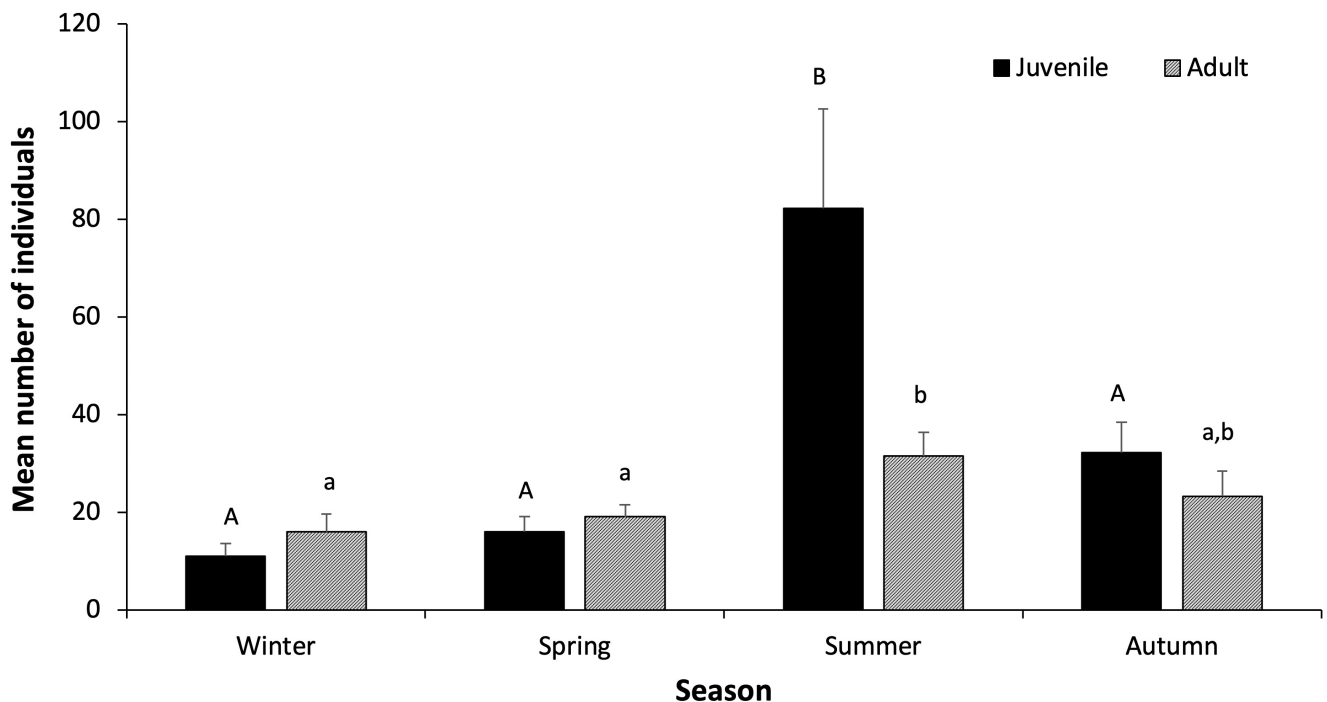

Figure 2. Mean number of juvenile (black bars) and adult (diagonal-hatched bars) spiders collected at the seven study sites within Te Paki Ecological District during winter, spring, summer and autumn. Error bars represent the standard error of the mean. Significant mean differences are indicated by different letters (upper case for juveniles and lower case for adults).

Table 1. Observed species richness, numbers of individuals captured, estimated species richness (Chao-2 and ICE) and species diversity indices (Simpson and Shannon–Weiner) of spiders at the seven study sites within Te Paki Ecological District.

| Site	Species richness[1]	Number of individuals[2]	Singletons	Doubletons	Chao-2[3]	ICE[3]	Simpson[4]	Shannon[5]
Tapotupotu (A)	15	115	1	1	15.0	15.4	0.9111	2.416
Tapotupotu (B)	22	113	9	2	31.8	34.3	0.9202	2.558
Shenstone Block	13	68	3	3	14.8	15.7	0.8507	2.054
Kohuroa (B)	19	147	6	3	22.7	25.9	0.7819	2.024
Te Huka (B)	19	197	6	3	25.1	28.3	0.6180	1.556
Haupatoto	15	226	2	2	15.7	16.8	0.7565	1.844
North Cape	16	125	4	1	17.8	18.5	0.8994	2.355
All sites	42	991	8	5	52.7	57.1	0.8737	2.717

[1]Observed species richness over the four seasonal samples.
[2]Total number of individuals (adult plus juvenile) identified to species over the four seasonal samples.
[3]Species richness estimators: Chao-2 and ICE (incidence-based coverage estimator).
[4]Simpson Index of Diversity ($1 - D$).
[5]Shannon–Wiener Species Diversity Index (H').
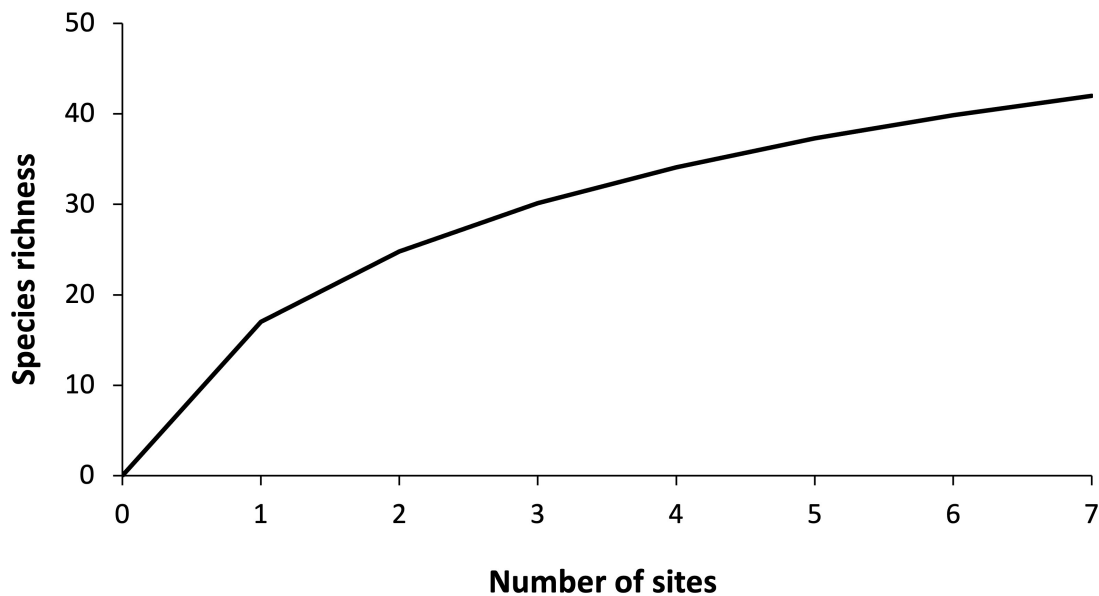
Figure 3. Sample-based rarefaction curve for the spider fauna at all seven study sites within Te Paki Ecological District over the four seasonal samples.

near the bottom of the plot. Of the more abundant taxa, spiders highly correlated with Axis 1 were *Rinawa* sp., *Porrhothele* sp., *Uliodon* sp., *Pahoroides balli*, and *Hulua convoluta* in the positive direction and *Cambridgea reinga*, *S. hollowayi*, and *H. apicus* in the negative direction. Abundant taxa correlated with Axis 2 included the undescribed zoropsid in the positive direction and *Episinus* sp. and *Paramamoea pandora* in the negative direction. However, Axis 2 explained a much smaller portion of the variability in the data than Axis 1.

Correlations of environmental variables with Axes 1 and 2 of the spider PCoA showed that plant species such as nīkau, pūriri, supplejack (*Ripogonum scandens*), kiekie (*Freycinetia banksii*), and karaka were positively correlated with Axis 1 (i.e. on the right side of the plot) and therefore more prevalent at sites such as Haupatoto, Te Huka (B), and Kohuroa (B) (Fig. 6). The mean top height of the vegetation, soil calcium concentrations, and soil pH also increased at these sites. In contrast, species such as twiggy coprosma (*Coprosma rhamnoides*), tī ngahere (*Cordyline banksii*), rārahu (*Pteridium esculentum*), pōhuehue (*Muehlenbeckia complexa*), and brush wattle (*Paraserianthes lophantha*), as well as the percentage ground cover of vegetation were strongly negatively correlated with Axis 1. Such conditions therefore prevailed at Shenstone Block and North Cape on the left of the plot, where the vegetation was also shorter.

The PCoA based on plant communities captured a strong gradient along Axis 1, which explained a substantial amount of the variation (60.9%) in the input data (Fig. 7). Plant
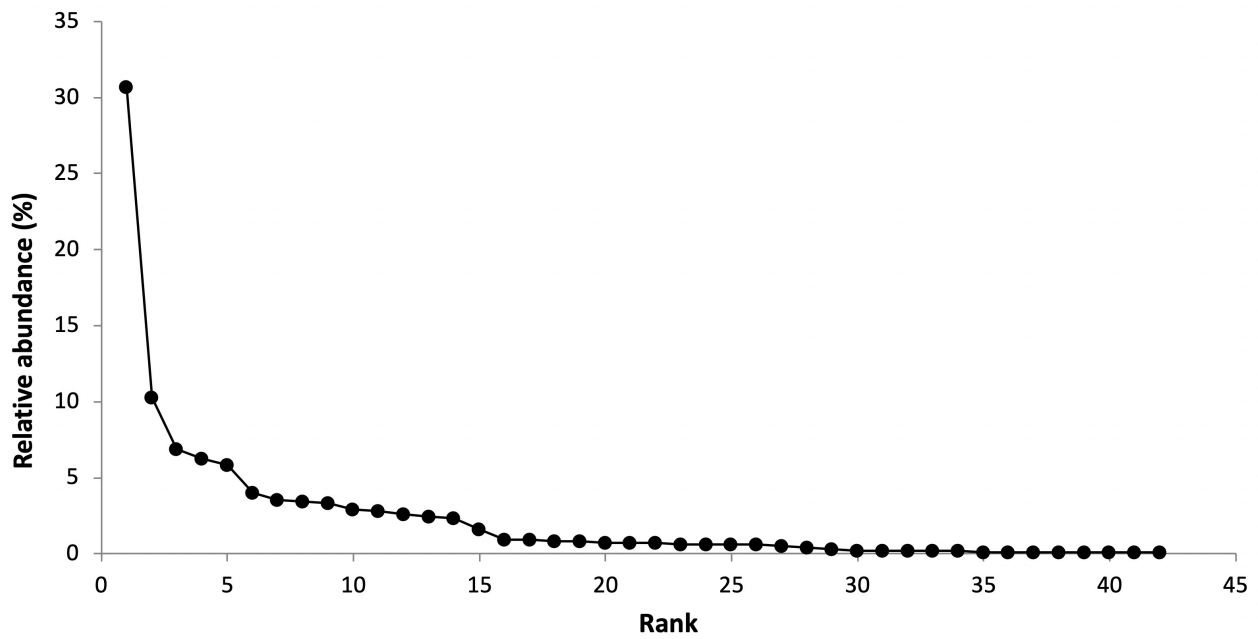
Figure 4. Rank–abundance plot of spiders recorded at all seven study sites within Te Paki Ecological District over the four seasonal samples.
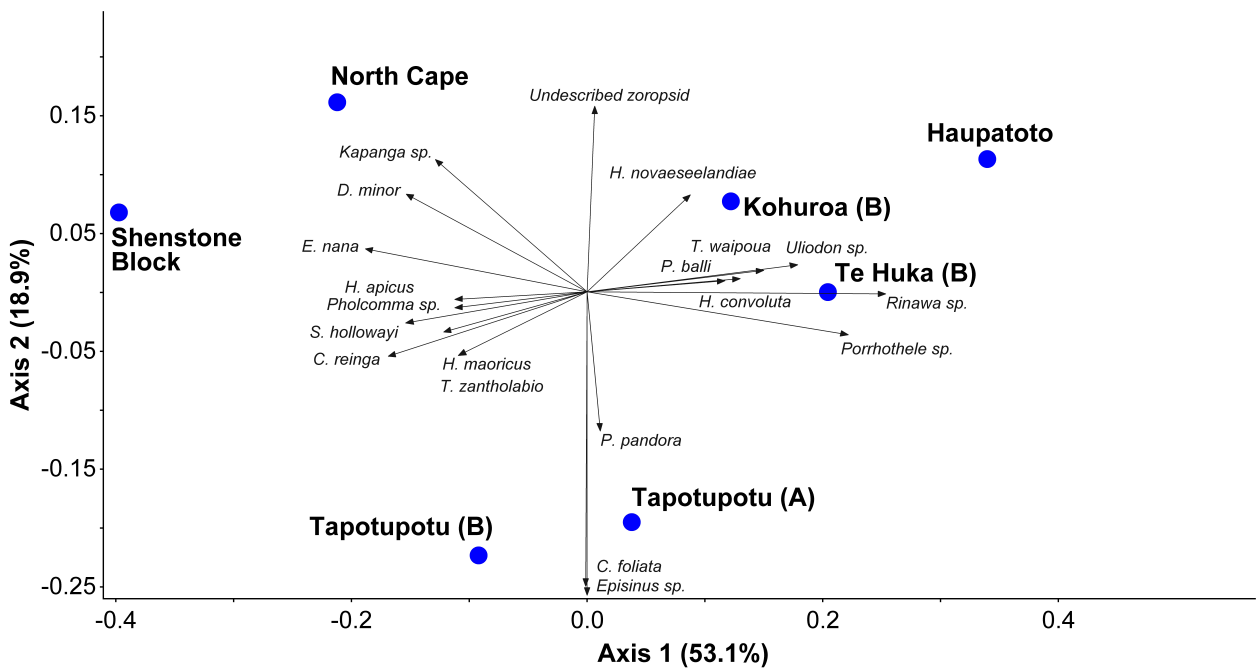

Figure 5. Principal coordinates analysis (PCoA) plot of the seven study sites within Te Paki Ecological District based on spider counts ($\log_{10}(x+1)$). Sites in close proximity have similar spider communities, whereas sites further apart have less similar spider communities. Overlay illustrates the spider species most correlated with the ordination axes (Pearson's r^2 cut-off = 0.4). Vectors indicate the strength and direction of correlations of the spider taxa that contributed most strongly to the gradients reflected by each ordination axis. See Appendix S2 for full species names.
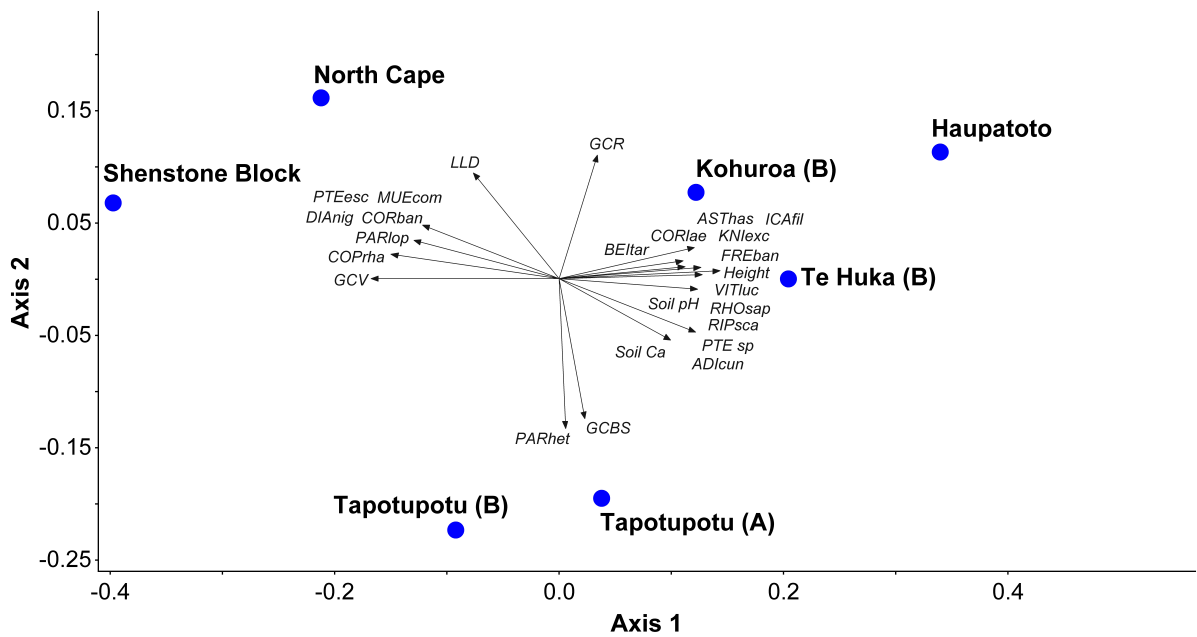
Figure 6. Principal coordinates analysis (PCoA) plot of the seven study sites within Te Paki Ecological District showing the relationship between the ordination scores of sites in spider space and the measured environmental variables. Overlay illustrates the environmental variables most correlated with the ordination axes (Pearson's r^2 cut-off = 0.6). Vectors indicate the strength and direction of correlations between environmental variables and axis scores. Environmental variables: *ADIcun = Adiantum cunninghamii*; *ASThas = Astelia hastata*; *BEItar = Beilschmiedia tarairi*; *COPrha = Coprosma rhamnoides*; *CORban = Cordyline banksii*; *CORlae = Corynocarpus laevigatus*; *DIAnig = Dianella nigra*; *FREban = Freycinetia banksii*; *GCBS* = ground cover bare mineral soil; *GCR* = ground cover rock; *GCV* = ground cover herbaceous vegetation; *Height* = mean top height of vegetation; *ICAfil = Icarus filiformis*; *KNIexc = Knightia excelsa*; *MUEcom = Muehlenbeckia complexa*; *LLD* = leaf litter depth; *PARhet = Parsonsia heterophylla*; *PARlop = Paraserianthes lophantha*; *PTEesc = Pteridium esculentum*; *PTE sp = Pteris* sp; *RHOsap = Rhopalostylis sapida*; *RIPsca = Ripogonum scandens*; *Soil Ca* = soil calcium concentration; *Soil pH* = pH of soil; *VITluc = Vitex lucens*.
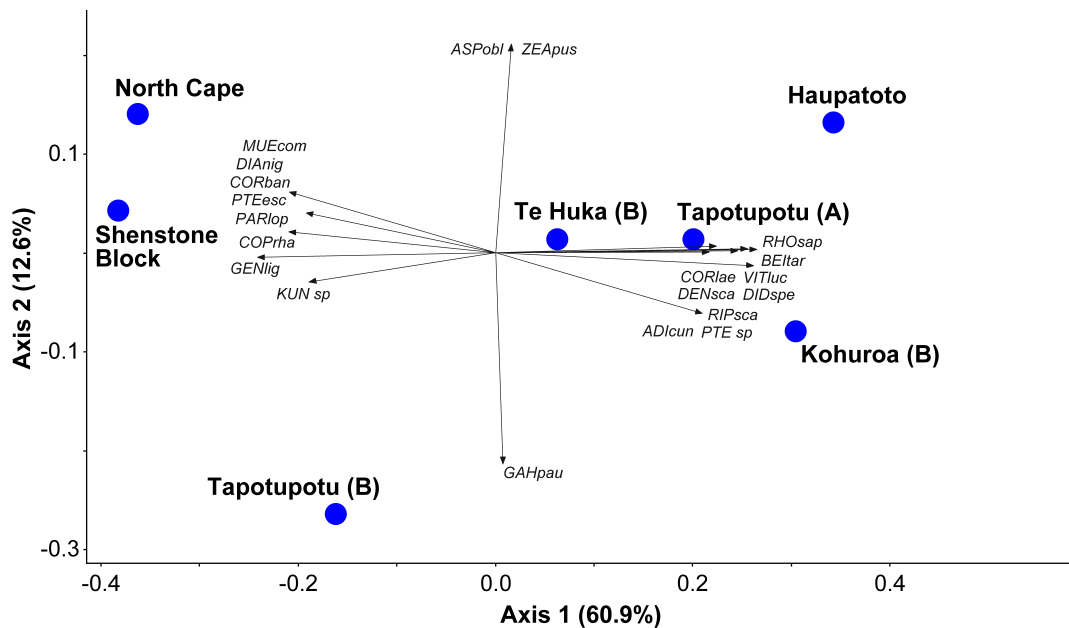

Figure 7. Principal coordinates analysis (PCoA) plot of the seven study sites within Te Paki Ecological District based on plant importance values. Sites in close proximity have similar plant communities, whereas sites further apart have less similar plant communities. Overlay illustrates the plant species most correlated with the ordination axes (Pearson's r^2 cut-off = 0.6). Vectors indicate the strength and direction of correlations between environmental variables and axis scores. Plant species: *ADIcun = Adiantum cunninghamii*; *ASPobl = Asplenium oblongifolium*; *BEItar = Beilschmiedia tarairi*; *COPrha = Coprosma rhamnoides*; *CORban = Cordyline banksii*; *CORlae = Corynocarpus laevigatus*; *DENsca = Dendroconche scandens*; *DIAnig = Dianella nigra*; *DIDspe = Didymocheton spectabilis*; *GAHpau = Gahnia pauciflora*; *GENlig = Geniostoma ligustrifolium*; *KUN sp = Kunzea* sp.; *MUEcom = Muehlenbeckia complexa*; *PARlop = Paraserianthes lophantha*; *PTEesc = Pteridium esculentum*; *PTE sp = Pteris* sp; *RHOsap = Rhopalostylis sapida*; *RIPsca = Ripogonum scandens*; *VITluc = Vitex lucens*; *ZEApus = Zealandia pustulata*.

species most strongly correlated with Axis 1 in the positive direction (i.e. on the right side of the plot) included nīkau, pūriri, karaka, taraire, and kohekohe. Such communities were most prevalent at Haupatoto and Kohuroa (B), and to a lesser extent at Tapotupotu (A) and Te Huka (B). Plant species negatively correlated with Axis 1 included hangehange, twiggy coprosma, tī ngahere, rārahu, pōhuehue, and kānuka. The plant communities at Shenstone Block, North Cape, and to a lesser extent Tapotupotu (B) on the left side of the plot were therefore dominated by these species.

Mantel tests showed that differences in spider community composition were significantly associated with changes in plant community ($r = 0.74$, $P < 0.01$), but were not strongly associated with geographic location ($r = 0.14$, $P = 0.24$).

Spider richness was not correlated with plant species richness or with most of the remaining biotic and abiotic environmental variables tested. Only soil organic matter content was significantly positively correlated with spider richness ($\tau = 0.72$, $P < 0.05$).

Discussion

Environmental correlates of spider communities

As we predicted, changes in forest spider communities were related to differences in plant composition, which in turn, appear to be related to the apparent seral stage of the forest remnant. Our findings broadly mirror those of Bultman et al. (1982) who recorded changes in spider communities along a successional forest gradient in the northern hemisphere. The ordination of sites in spider space captured both gradients and divisions in spider communities. Correlations of the measured predictor variables with Axis 1 of the ordination in spider space (Fig. 6) showed that spider communities at the sites on the right side of the plot were strongly affiliated with taller vegetation, plant species such as pūriri, nīkau, kiekie, karaka, and taraire, and soils with higher pH and calcium concentrations. In contrast, spider communities at sites on the left side of the plot were associated with shorter vegetation, more forest floor vegetation, and plant species such as twiggy coprosma, tī ngahere, rārahu, pōhuehue, and brush wattle. The ordination of sites in plant space (Fig. 7) produced a very similar plot with respect to the arrangement of the study sites. The same study sites on both sides of the plot were therefore strongly associated with the same plant species, with the addition of kohekohe on the right side of the plot and kānuka on the left. This close association between the spider and plant communities was confirmed by the significant Mantel test result. The plant species and conditions to the right of the ordination plots are those most associated with later seral stages of New Zealand forests. These environments were therefore most clearly manifested at Haupatoto and Kohuroa (B), and to a lesser extent Tapotupotu (A) and Te Huka (B), whose spider communities tended to be dominated by species such as *Rinawa* sp., *Porrhothele* sp., *Uliodon* sp., *Tangata waipoua*, *P. balli*, and *H. convoluta* (Fig. 5). Conversely, the plant communities and conditions associated with the left side of Figures 6 and 7 are more representative of transitional or disturbed forest ecosystems at earlier seral stages. These types of environments were therefore most evident at Shenstone Block, North Cape, and to a lesser degree at Tapotupotu (B), where spiders such as *Euryopis nana*, *C. reinga*, *S. hollowayi*, and *H. apicus* predominated (Fig. 5). Not surprisingly, some species on the left side of the plot in spider space such as *E. nana* and *Dolomedes minor*

are known from scrubby habitats too, the latter apparently avoiding deep forest altogether (Forster & Forster 1999; Vink & Dupérré 2010).

Thus, even though native forest would be considered a principal habitat for most of the species (or their nearest kin) detected in the study (Forster & Wilton 1968, 1973; Forster 1970; Forster & Blest 1979; Forster & Forster 1999; Paquin et al. 2010; Fitzgerald & Sirvid 2011), many taxa displayed clear affinities along a continuum from open scrubby forest at earlier seral stages to closed broadleaf forest at later seral stages. This study therefore provides insights into some of the potentially useful bioindicator species of ecological restoration and succession, in particular *Rinawa* sp. and *Uliodon* sp. in forest at later seral stages and *C. reinga* and *S. hollowayi* in forest likely to be at earlier seral stages. These species were commonly trapped at sites where conditions were favourable (i.e. with respect to vegetation type and seral stage), and were either not detected, or captured in very low numbers where conditions were likely unfavourable. It is important to remember that the apparent seral stage of the vegetation at all of the sites is dependent upon a range of factors, the most critical of which are likely to be history of disturbance (mainly burning), substrate, and other environmental variables such as coastal influence (Lux et al. 2009). Ultimately, it is the structure of the habitat that probably plays the most critical role in shaping spider communities (Uetz 1991; Wise 1993), so our results should be considered in this context.

Correlates of spider richness and diversity

Of the biotic and abiotic predictor variables tested, only soil organic matter content was significantly (positively) correlated with spider richness. The implications of this result are difficult to expand upon as there was no evidence of significant associations between spider richness or diversity and any of the other measured predictor variables, or with Axis 1 of the PCoA in spider space (Fig. 5). Thus, contrary to our prediction, spider richness and diversity were not positively associated with plant composition or estimated seral stage. There is evidence from overseas studies that spider communities can show a "pre-climax" peak in species diversity (e.g. Bultman et al. 1982). However, the inherent difficulties in adequately defining what constitutes "climax" or "pre-climax" vegetation make such conclusions challenging and risky. It is possible that the differences in the measured biotic and abiotic factors between the seven sites were too subtle and subject to too much variation for significant effects to emerge, in which case, more replicate sites would be needed to determine whether associations exist or not. Furthermore, in our study, there is evidence of undersampling bias (see discussion below), and the ramifications of this in generating less reliable species richness totals should be acknowledged (Longino et al. 2002; Scharff et al. 2003).

Our findings in relation to potential drivers of spider richness should be seen in the context of previous studies, where associations with biotic and abiotic predictor variables similar to those assessed in our study are sometimes significant (Uetz 1975, 1979; Coyle 1981; Jiménez-Valverde & Lobo 2007; Finch et al. 2008; Malumbres-Olarte et al. 2013b; Štokmane & Spuņģis 2016), and sometimes not (Harris et al. 2003; Grill et al. 2005; Baldissera et al. 2008; Schuldt et al. 2008). Some of this inconsistency no doubt stems from substantial differences in the scope of the various studies in relation to factors such as spider guild, nature of the habitat(s) under investigation, detection methods, scale, and possibly

undersampling bias. Nevertheless, it is evident that spider richness is most likely determined by a complex interaction of environmental and temporal factors that operate at different spatial scales. Moreover, covariance of explanatory variables makes identification of the actual causal factors even harder (Uetz 1975, 1979; Mac Nally 2000; Tews et al. 2004; Finch et al. 2008).

Overall spider abundance and diversity

The epigeal spider fauna in native forest at TPED was dominated by representatives from the Hahniidae and Zoropsidae, and to a lesser extent Gnaphosidae. The dominance of these families is attributable to the presence of one particularly abundant species in each family, *Rinawa* sp. (Hahniidae), *Uliodon* sp. (Zoropsidae), and *H. apicus* (Gnaphosidae), rather than being the most species diverse. Our results are quite different from pitfall trap studies of epigeal spiders in native forest from other parts of New Zealand where representatives from families such as Agelenidae, Amaurobiidae, Anapidae, Cycloctenidae, Desidae, and Megadictynidae, as well as Zoropsidae, tend to dominate (Berndt 1998; Alley et al. 2001; Sinclair et al. 2005; Lamont et al. 2017). Thus family, and therefore species-level differences in epigeal spider communities from native forest in different parts of the country can be quite marked, notwithstanding that such differences are often due to the presence of one or two particularly abundant species in those families. However, species abundance distributions appear to be more homogeneous. Our rank–abundance distribution was very similar to the distribution of Lamont et al. (2017) for pitfall trapped spiders at Boundary Stream, Hawke's Bay, and shows that a small number of very abundant species tend to dominate communities, whereas for most species, very few individuals are trapped. This is a frequently observed pattern in many community data sets (Williams 1964) and presumably signifies a consistency in the underlying ecological processes shaping these assemblages (Magurran 2004).

There was significant temporal variation in abundance of both adult and juvenile spiders when all taxa are combined (the phenology of individual species will be addressed elsewhere). Both juvenile and adult stages were detected in the highest numbers during the summer survey. Presumably, the peak in summer is a consequence of increased activity and abundance and is also indicative of the timing of the reproductive cycle for most taxa. Studies in different forest types in the Orongorongo Valley near Wellington showed peaks in spider numbers in autumn and summer where pitfall trapping and Tullgren funnel extraction of leaf litter were used as the detection methods respectively (Moeed & Meads 1985, 1986).

Sampling factors

The sample-based rarefaction curve and most of the species richness estimates indicate that the species inventory for our study was incomplete. It was estimated that the total observed species richness represented 74–80% of the true epigeal spider fauna present at the sites. This is similar to the range seen in other spider and invertebrate community studies in New Zealand for which data are available (Affeld et al. 2009; Ward et al. 2014; Lamont et al. 2017). The species deficit is due to the prevalence of species caught in very low numbers, in particular singletons (19%) and doubletons (12%), relative to the more common species. Similarly high frequencies of singletons and doubletons were reported in New Zealand studies by Lamont et al. (2017) for spiders, and for beetles by Ward et al. (2014). They are also comparable to frequencies

of singletons from various studies of tropical arthropod taxa (Coddington et al. 2009).

Coddington et al. (1996, 2009) and Scharff et al. (2003) discussed several "edge" effects as potential causal factors for the high incidence of species caught in very low numbers. They argued that some species may appear rare because the habitat sampled, and the time and method of sampling, are not well matched with their ecology. This is undoubtedly the case for several of our low abundance species including *Cambridgea foliata* and *D. minor*. However, the prevalence of at least some of the uncommon species should be interpreted as undersampling bias (Scharff et al. 2003; Coddington et al. 2009). Despite the fact we sampled seasonally and included both adults and juveniles, the evidence of undersampling bias indicates our investigation would have benefited from more replication. A more temporally and spatially comprehensive sampling programme that also accounted for other natural cycles such as moon phase and El Niño-Southern Oscillation would have likely improved the study. However, more intense sampling would need to be balanced against the negative impacts this has on invertebrate populations.

Conservation and other study implications

Our investigation supports the view that TPED is an area of high biodiversity value and a centre of endemism for spiders. Of the 42 species detected here, 15 (36%) are likely to be TPED endemics. Comparable rates of regional endemism have not been observed in any other study involving spider communities in indigenous New Zealand ecosystems (Alley et al. 2001; Derraik et al. 2001; Michel et al. 2008; Malumbres-Olarte 2010; Malumbres-Olarte et al. 2013a, 2013b; Lamont 2017). For four of these species (*C. reinga*, *Gasparia tepakia*, *Novalaetesia anceps*, and *S. hollowayi*) only one sex was available for the original descriptions. Forster and Wilton (1973) described the female of *C. reinga*, and later Blest and Vink (2000) described the male of a "closely related species", *Nanocambridgea grandis*. Only when spiders from our study were examined was *N. grandis* recognised as the male of *C. reinga* and the male and female were reunited and redescribed (Vink et al. 2011). This study has also provided the first specimens of the female of *G. tepakia* and the male of *N. anceps* and *S. hollowayi*. Furthermore, 10–15 undescribed species of spider, including *Rinawa* sp., *Haplinis* sp., *Kapanga* sp., and an undescribed zoropsid spp. were collected (see Appendix S3 of Supplementary Materials for brief notes on these). This indicates that there is still a significant lack of knowledge concerning the taxonomy and ecology of many spiders, and not only those endemic to TPED. Moreover, several of these species were recorded at only one or two sites, potentially indicating restricted distributions.

This study demonstrates the immense value of biodiversity surveys. It has increased our understanding of (1) the spider assemblages in the area, (2) how spiders interact with plant communities and the environment, (3) the potential use of spiders as bioindicators, (4) the conservation value of the study sites, and (5) spider taxonomy in general. Simultaneously however, it has increased our appreciation of how much is still unknown. Given the extent of the taxonomic impediment and the high levels of endemicity amongst the spiders and other invertebrates in TPED, we call urgently for a strategic and comprehensive reappraisal of research there that is also in-line with the environmental goals of the local iwi and hapū.

Acknowledgements

Data Availability

A summary of the raw data is presented in Appendices S1 and S2. There are no additional publicly available raw data associated with this article.

Author contributions

OJPB and PTW designed the project. SRP, OJPB and PTW contributed to the fieldwork. SRP and OJPB separated spiders from other invertebrates and BMF identified the spider material. PTW and OJPB oversaw resourcing for the project. All authors contributed to the production of the manuscript.

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Summary of the physical, chemical, and biological attributes of the seven study sites.

Appendix S2. Total numbers of spiders (adult/juvenile) of all species/taxa captured during the four seasonal pitfall trapping surveys at the seven native forest sites across Te Paki Ecological District.

Appendix S3. Notes on spiders of uncertain taxonomic status collected during this study.

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