

SHORT COMMUNICATION

Native and adventive detritivores (Diplopoda, Isopoda and Amphipoda) in a modified landscape: influence of forest type and edge

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Abstract: The distribution and prevalence in New Zealand of adventive detritivores in native forest remnants, and of native detritivores in pine plantations, are not well known. We investigated whether forest type (small urban native remnants, large remote native remnants, and pine) and plot location (edge plot vs centre plot) influenced the abundance and community composition of native and adventive detritivores (Diplopoda, Isopoda, and Amphipoda) in forests of a modified landscape in the lower North Island of New Zealand. We found that a number of adventive taxa have spread throughout native forests in the region. Two species of adventive Diplopoda – *Cylindroiulus britannicus* (Verhoeff, 1891) and *Ophiulus pilosus* (Newport, 1842) – were especially widely distributed and found at high abundance. Adventive Diplopoda were more abundant in native than in pine forests. Plot location (edge vs centre) did not affect the abundance of detritivores. An adventive *Arcitalitrus* sp. was the dominant Amphipoda in small native forest remnants in urban locations; it was also the only Amphipoda present in the majority of pine forests. Almost no adventive Isopoda were found. There was no effect of forest type on abundance of native Diplopoda and most native Isopoda, whereas native Amphipoda preferred large remote native forest remnants. Overall, pine forests supported as many native detritivores as native forests, confirming that pine forests contribute to preserving native biodiversity.

Keywords: edge effects; exotic species; forest biodiversity; fragmentation; macrofauna

Introduction

New Zealand's biota is characterised by the large number of adventive invertebrate species (Brockhoff et al. 2010). Some adventive invertebrates have been observed deep within native forests (Tomlinson 2007; Kelly & Sullivan 2010), yet others appear to be rare or absent in native forests despite being present in adjacent disturbed habitats (Harris & Burns 2000; Pawson et al. 2008).

It has been proposed that New Zealand's native forests may be resistant to invasion and establishment of some adventive invertebrates, e.g. ground-dwelling beetles (Harris & Burns 2000; Pawson et al. 2008) and host-specific invertebrate herbivores (Brockhoff et al. 2010). In the case of host-specific herbivores, New Zealand's endemic flora is frequently phylogenetically distant from their host plants, which limits their invasion (Brockhoff et al. 2010). However, this mechanism is unlikely to influence food generalists, such as many detritivores. Among trophic guilds, detritivores may be better able to colonise and exploit newly available niches (Samways et al. 1996; Hoare 2001). There is evidence that invertebrate detritivores may be more successful at invading New Zealand's native forests than other trophic groups. For example, multiple studies have reported adventive detritivores in New Zealand's native forests, often at high abundance (Johns 1995; Harris & Burns 2000; Tomlinson 2007). Adventive Diplopoda have been found throughout native forests, in small remnants as well as in large reserves (Dawson 1958; Tomlinson 2007; Costall 2012). The adventive moth *Opogona omoscopia* (Meyr., 1893) (Tineidae) (which in its larval stages feeds as a detritivore in leaf litter) was the dominant invertebrate in

leaf litter in the large tract of native forest in the Waitakere Ranges (Tomlinson 2007).

Detritivores comminute plant litter, consume detritus, mix soil, and alter decomposition rates and soil microbial communities (Moore et al. 1988; Mikola et al. 2002). For example, Amphipoda (Crustacea: Talitridae) make up a large part of the soil and leaf litter fauna in New Zealand forests and can occur at very large densities, indicating that they play a significant role in shredding forest leaf litter (Fenwick & Webber 2008). Despite the recognised importance of soil detritivores to ecosystem function, detritivores are not frequently or sufficiently studied in New Zealand. The knowledge of the native fauna remains incomplete; the distribution and abundance of adventive detritivores are not recorded sufficiently, and their possible impacts on New Zealand's native forests have not been investigated (Brockhoff et al. 2010).

An unknown variable in the state of detritivore biodiversity is their use of pine plantations, a significant industry in New Zealand with *Pinus radiata* covering 1.73 million ha (Ministry for Primary Industries 2013). There is still little information on non-insect detritivores in pine plantations (e.g. Minor 2011). It is not clear to what extent adventive detritivore species colonise pine plantations, and whether native species are able to utilise the pine forest resources.

We examined the distribution of native and adventive detritivores (Diplopoda, Isopoda, and Amphipoda) in forests of a modified landscape in the lower North Island of New Zealand. We considered three types of forest (small urban native remnants, large remote native remnants, and pine forests), as well as edge vs centre plots at each site, since exotic species

are often associated with edges (Hickerson et al. 2005). The following questions were asked: (1) How prevalent are adventive detritivores in native forest remnants in the region? (2) Do pine plantations provide alternative habitat for native forest detritivores? (3) Does the type of forest and proximity to the forest edge influence the abundance and community composition of native and adventive detritivores?

Methods

Sites and sampling

Invertebrates were collected from 10 native and 6 pine forests in the Manawatu-Wanganui region, North Island of New Zealand (Fig. 1). Native forests ranged from smaller urban remnants (< 30 ha, *n* = 6) to larger more remote remnants (> 60 ha, *n* = 4); see online Appendix S1 for descriptions of the study sites.

The sites were sampled from March to October 2012; each site was sampled once (see Appendix S1 for sampling dates). To ensure consistency in sampling conditions, samples were not collected following heavy rainfall. At each site, two plots were selected: one within 20 m of the forest edge and another in a more central location (at least 100 m away from the edge unless in very small remnants that did not allow this distance). Sampling plots were chosen preferentially on flat ground; if this was not available then a site with only minimal slope was chosen. GPS coordinates and a list of dominant plant species were collected from each plot. The plant surveys were not a comprehensive list of all plant species in a plot, but are recorded (see Appendix S1) to give some background information.

We collected two sets of samples. First, detritivores were collected from fallen logs within a 10 × 10 m quadrat at the centre of each plot. Logs were placed on a white sheet one at a time, and any Diplopoda, Isopoda, or Amphipoda found on

the exterior of the log, under the bark (if bark was present) or any that fell onto the white sheet were collected into 70% alcohol. A ‘log’ was considered to be any fallen wood with a circumference > 25 cm. Very large logs, which could not be lifted onto the white sheet, were excluded from the study. Logs only partly in the quadrat were sampled if the majority of the log lay within the quadrat.

Second, five leaf litter samples were collected from the exterior of each log-sampling quadrat at haphazard locations within 3 m from any quadrat edge. Collecting leaf litter from outside the log-sampling quadrat ensured the litter had not been disturbed prior to sampling. Leaf litter was collected within a 25 × 25 cm metal sampling frame placed on the forest floor and pressed down 1 cm into the soil layer. The litter was stored in sealed plastic bags at 4°C until extraction. The samples were extracted in Berlese–Tullgren funnels until completely dry. The invertebrates were stored in 70% alcohol.

Sorting and identification

Adventive Diplopoda, Isopoda, and Amphipoda were identified to species level. Identification of many native taxa to levels beyond order/family was difficult, in which case native detritivores were identified to a level that provided differentiation from adventive taxa. Some specimens of Polydesmida millipedes (Diplopoda) and Amphipoda were unidentifiable (either damaged or too young) and were excluded from analysis.

Diplopoda were identified to order level using keys by Johns (1962) and Hoffmann (1990). Mesibov (2003) was used in combination with Blower (1985) to identify adventive Julida. Among Polydesmida both native and adventive species are present in New Zealand. We have grouped Polydesmida (including females and juveniles) into morphospecies. Gonopods of mature male Polydesmida were compared with

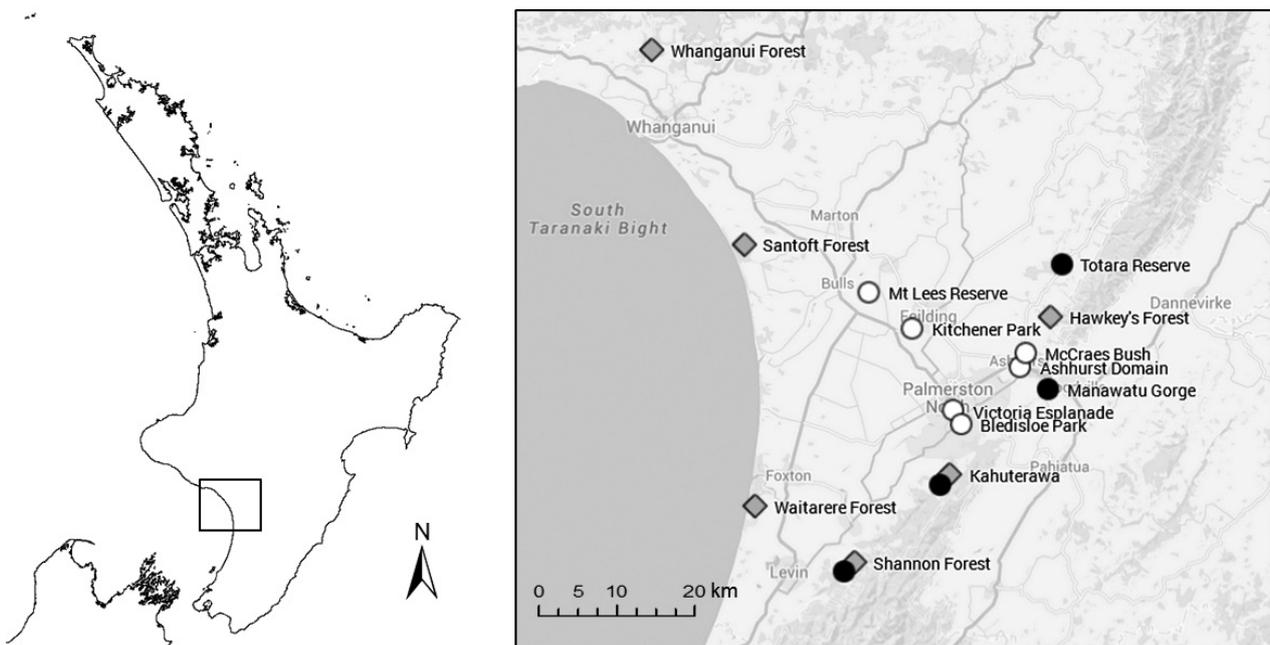


Figure 1. Sampling sites in the Manawatu-Wanganui Region, North Island of New Zealand, 2012 (adapted from Google maps). Open circles – small urban native remnants; closed circles – large remote native remnants; diamonds – pine forests.

illustrations from Mesibov (2003) and Blower (1985), and individuals were presumed to be native if they did not match the description of the five adventive Polydesmida species recorded to be present in New Zealand (Johns 2010). Female and juvenile Polydesmida are difficult to identify (Mesibov 2003), and when no males were present, Polydesmida were recorded as 'unknown'.

Isopoda were identified to family level using an unpublished key by Stefano Taiti (S. Taiti, pers. comm. 2012). Adventive families were identified to species level using primary descriptions. The family Armadillidae, which includes many native species, also includes an adventive species, *Cubaris murina* Brandt, 1833. Therefore, Armadillidae were compared with the primary description of *C. murina*.

Amphipoda were identified to species level using Fenwick & Webber (2008), although there was difficulty identifying *Arcitalitrus* past genus level. There are two closely related species of *Arcitalitrus* in New Zealand, *A. sylvaticus* (Haswell, 1880) and *A. dorrieni* (Hunt, 1925), both introduced from Australia (Fenwick & Webber 2008). The two species are not easily distinguished (R. Webber, pers. comm., 2013), so they were not separated here. However, *Arcitalitrus* in our study is probably *A. sylvaticus*, because *A. dorrieni* has not been found in the lower North Island (Fenwick & Webber 2008). Samples were sent to R. Webber (Te Papa Tongarewa Museum, Wellington) to confirm identification.

Statistical analysis

For presentation of results, abundance values in leaf litter were standardised to individuals per square metre to make them more comparable with past and future work. The abundance trends in logs and litter were similar, so, for further analysis, abundance in each edge or centre plot was calculated as the total number of individuals found in all five leaf litter samples plus the individuals from logs within the 100-m² quadrat. SAS® 9.3 software (SAS Institute) was used to calculate descriptive statistics and to perform analysis. A generalised linear mixed model (PROC GLMMIX), using a negative binomial distribution and the quadrature method of likelihood estimation, was applied to test the effect of forest type and plot location (edge vs centre) on the abundance of each detritivore group (Isopoda, Diplopoda and Amphipoda), as well as on the abundance of individual families and species. Forest type and plot location were fixed effects in the model; site identity was considered a random factor to account for differences across sites, such as the age of pine plantations. For testing the forest type, all sites were divided into three groups: small native remnants (< 30 ha, $n = 6$), larger native remnants (> 60 ha, $n = 4$), and pine forests ($n = 6$). The small remnants were all urban sites, and the large remnants were more remote, so these two characteristics were confounded. The 'small native vs large native' and 'pine' vs 'native' effects were tested as a set of orthogonal contrasts.

A binary logit model was created (using the SAS GLMMIX logistic procedure) for each detritivore group to determine if forest type and plot location significantly influenced the probability that a randomly chosen individual would be adventive (i.e. 'adventive' was used as an 'event' in the model). The multi-response permutation procedures method (MRPP) in PC-Ord for Windows (MjM Software, version 5) was used to test the null hypothesis of no difference in community composition of detritivores between forest types (small native remnant, large native remnant, pine forest) and between plot locations. The data were square-root transformed to reduce

the importance of the most dominant taxa. If species-level classification was determined (e.g. for Julida and Amphipoda), the species were included in the analysis separately. The MRPP was applied to the species abundance matrix with the Bray–Curtis distance as the similarity measure. Groups with low abundance (< 5 individuals) were excluded. Habitat associations between groups of detritivores and forest type were analysed using the Indicator Species Analysis (IndVal) (Dufrene & Legendre 1997) in PC-Ord 5. Significance level $\alpha = 0.05$ was used for all statistical tests.

Results

Distribution and community composition of native and adventive detritivores

Polydesmida were the most abundant order of native Diplopoda in study forests, although less abundant than adventive Julida (Table 1). Polyzoniida were found in most native forests, but, along with Spirostreptida, were uncommon or absent under pine. Siphonophorida were found in 8 out of 10 native forests, but only in 2 out of 6 pine forests; yet in one of the pine forests they were the dominant Diplopoda group in leaf litter, reaching 246.4 individuals m⁻² in the edge plot. Only three specimens of Polyxenida were found. Five species of adventive Diplopoda from the order Julida were collected. *Cylindroiulus britannicus* (Verhoeff, 1891) was found in 9 out of 10 native forests and in 2 out of 6 pine forests, had the highest abundance of any adventive Diplopoda (up to 224 individuals m⁻² in leaf litter) throughout the study area, and in a number of sites was more dominant than the native Polydesmida. *Ophiulus pilosus* (Newport, 1842) was also widespread; it was found in 9 out of 10 native forests and in 5 out of 6 pine forests, although not at such high abundances as *C. britannicus*. *Brachyiulus pusillus* (Leach, 1815) was found in 3 native forests and in 2 pine forests, and *Blaniulus guttulatus* (Fabricius, 1798) was found only at two small urban native sites. Only one specimen of *Nopoiulus kochii* (Gervais, 1847) was found (Table 1).

Four native Isopoda families (Styloniscidae, Philosciidae, Armadillidae, Oniscidae) were identified from forests in Manawatu-Wanganui (Table 1). Two species of adventive Isopoda were found – *Armadillidium vulgare* (Latreille, 1804) (Armadillidiidae) and *Porcellio scaber* Latreille, 1804 (Porcellionidae) – both in very low numbers (Table 1).

Amphipoda of the adventive genus *Arcitalitrus* were found throughout Manawatu-Wanganui (Table 1), reaching high densities (up to 867.2 individuals m⁻² in leaf litter in Bledisloe Park). *Arcitalitrus* were present in all pine forests except Kahuterawa pine, in all native forests except Totara Reserve and Manawatu Gorge (both large remote remnants), and were the only Amphipoda present in five out of six small urban native remnants. In four native forests *Arcitalitrus* co-occurred with native Amphipoda. Native *Parorchestia tenuis* (Dana, 1852) was found in three larger, less disturbed native forests, where *Arcitalitrus* was absent or low in abundance. Another native landhopper, *Puhuruhuru aotearoa* Duncan, 1994, was sometimes the only Amphipoda at a site, or co-occurred with adventive *Arcitalitrus*; *Parorchestia tenuis* was never found in the absence of *Puhuruhuru aotearoa*. Both native Amphipoda were found in only one pine forest (Kahuterawa), where *Arcitalitrus* was absent.

Community structure of native and adventive detritivores was influenced by the forest type (MRPP: $A = 0.133$, $P <$

Table 1. Native and adventive Diplopoda, Isopoda and Amphipoda (individuals m⁻²) in leaf litter in forests of the Manawatu-Wanganui Region New Zealand, 2012. Values are mean ± standard error; ‘-’ = none found.

Taxa		Small urban native remnants	Large remote native remnants	Pine forests
DIPLOPODA				
Native	Chordeumatida	4.8 ± 1.92	6.02 ± 0.22	6.4 ± 3.76
	Polydesmida	17.34 ± 6.14	4.0 ± 0.86	2.93 ± 1.60
	Polyzoniida	16.0 ± 7.23	4.0 ± 2.46	1.87 ± 1.87
	Siphonophorida	1.06 ± 0.45	8.0 ± 4.61	24.53 ± 20.37
	Spirostreptida	-	3.20 ± 1.82	-
	Polyxenida*	-	-	-
Adventive	<i>Cylindroiulus britannicus</i>	29.34 ± 17.89	27.62 ± 14.18	3.47 ± 3.47
Julida	<i>Ophiulus pilosus</i>	28.26 ± 12.70	4.0 ± 2.08	9.87 ± 3.79
	<i>Brachyiulus pusillus</i>	2.94 ± 1.95	-	2.40 ± 2.13
	<i>Blaniulus guttulatus</i>	4.0 ± 2.69	-	-
	<i>Nopoiulus kochii</i>	0.26 ± 0.26	-	-
Unknown	Juveniles**	79.20 ± 31.30	39.20 ± 10.66	42.13 ± 20.56
Total Diplopoda		183.20 ± 82.53	96.04 ± 36.89	151.2 ± 57.55
ISOPODA				
Native	Styloniscidae	40.26 ± 11.9	46.82 ± 9.54	17.34 ± 6.29
	Philosciidae	22.94 ± 16.45	5.60 ± 3.71	3.20 ± 2.05
	Armadillidae	2.40 ± 1.06	0.80 ± 0.8	1.06 ± 1.06
	Oniscidae	-	4.80 ± 2.72	-
Adventive	<i>Armadillidium vulgare</i>	0.26 ± 0.26	-	-
	<i>Porcellio scaber</i> *	-	-	-
Total Isopoda		65.86 ± 29.67	58.02 ± 16.77	21.60 ± 9.4
AMPHIPODA				
Native	<i>Puhuruhuru aotearoa</i>	-	28.40 ± 10.74	5.60 ± 3.82
	<i>Parorchestia tenuis</i>	-	10.0 ± 5.18	16.0 ± 11.48
Adventive	<i>Arcitalitrus</i> sp.	184.54 ± 72.38	2.80 ± 1.53	73.33 ± 24.2
Total Amphipoda		184.54 ± 72.38	41.2 ± 17.45	94.93 ± 39.5

*Only found on logs.

**Juvenile Polydesmida not identifiable as native or adventive.

0.001) but not plot location ($A = -0.009$, $P = 0.897$). IndVal analysis identified detritivore groups and species significantly associated with the three forest types (observed Indicator Value > 50%). Small urban native remnants were characterised by the presence of adventive *Arcitalitrus* (IndVal = 56.5%, $P = 0.004$), *Cylindroiulus brittanicus* (59.0%, $P = 0.003$), and *Ophiulus pilosus* (55.5%, $P = 0.004$), as well as native Oniscidae (61.0%, $P = 0.001$). Large remote native remnants were characterised by the presence of native landhopper *Puhuruhuru aotearoa* (IndVal = 75.0%, $P = 0.001$) and Polydesmida morphospecies 5 (IndVal = 58.9%, $P = 0.002$). Pine forests were characterised by the presence of Polydesmida morphospecies 11 (IndVal = 54.5%, $P = 0.001$).

Abundance patterns

Overall, there was no difference in the abundance of native Diplopoda between pine and native forests ($F_{1,16} = 0.60$, $P = 0.450$), and between edge and centre plots ($F_{1,16} = 1.71$, $P = 0.210$). However, native millipedes were significantly more abundant in small urban native remnants compared with large remote ones ($F_{1,16} = 5.89$, $P = 0.028$) (Fig. 2a). Adventive Diplopoda were more abundant in native forests than in pine ($F_{1,16} = 7.51$; $P = 0.014$); this was a reflection of

the distribution of *Cylindroiulus britannicus*, which was the only adventive millipede influenced by forest type, and which was much more abundant in native forests ($F_{1,16} = 14.05$; $P = 0.001$). For native forests, abundance of adventive millipedes in small urban remnants and large remote remnants was similar ($F_{1,16} = 1.51$, $P = 0.236$). No pattern was seen for plot location except that samples from edge plots had a greater range in abundance (Fig. 2b). The logistic regression model suggested that forest type ($F_{2,28} = 33.59$, $P < 0.001$) significantly affected the probability of a randomly collected Diplopoda individual being adventive. It was more likely that any millipede found would be adventive if it was found in a small urban native forest (Table 2).

Abundance of native landhoppers was significantly higher in large remote native forests ($F_{1,16} = 9.20$, $P = 0.008$) (Fig. 2c), though plot location had no effect. Similarly, plot location had no influence on the abundance of adventive *Arcitalitrus*, but forest type had a significant effect, with much higher abundances in small urban native forest remnants ($F_{1,16} = 32.75$, $P < 0.001$) (Fig. 2d). *Arcitalitrus* were found at higher abundances than native Amphipoda across all habitat types. Forest type ($F_{2,25} = 76.39$, $P < 0.001$) influenced the probability that a randomly collected Amphipoda individual would be

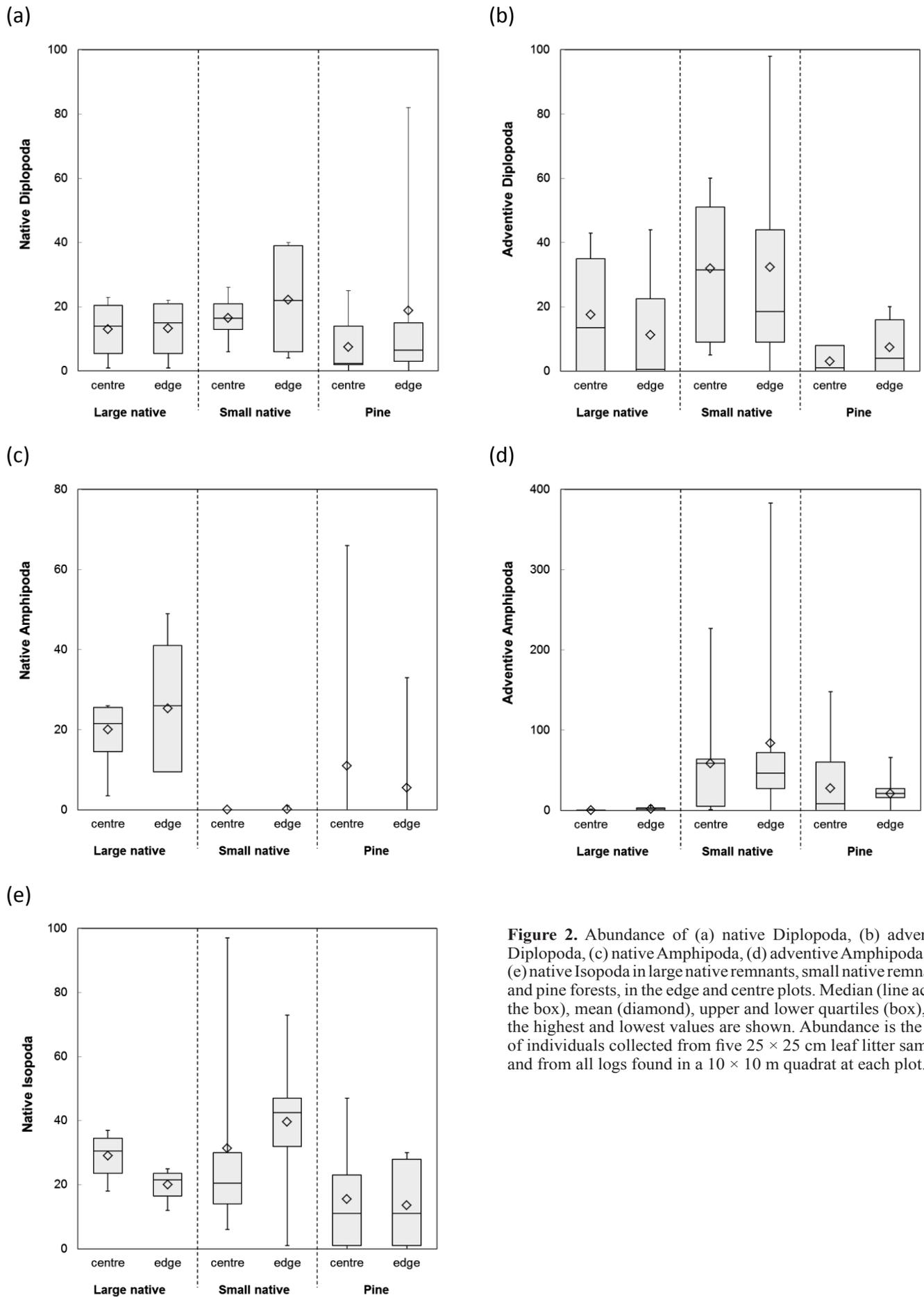


Figure 2. Abundance of (a) native Diplopoda, (b) adventive Diplopoda, (c) native Amphipoda, (d) adventive Amphipoda, and (e) native Isopoda in large native remnants, small native remnants, and pine forests, in the edge and centre plots. Median (line across the box), mean (diamond), upper and lower quartiles (box), and the highest and lowest values are shown. Abundance is the sum of individuals collected from five 25 × 25 cm leaf litter samples and from all logs found in a 10 × 10 m quadrat at each plot.

Table 2. Probabilities (\pm SE) that a randomly collected individual would be adventive depending on forest type. Logistic regression in GLMMIX for forest type and plot location (forest edge vs centre), Diplopoda: $P < 0.001$ for forest type, $P = 0.426$ for plot location, Amphipoda: $P < 0.001$ for forest type, $P = 0.448$ for plot location.

	Large remote native remnants	Small urban native remnants	Pine forests
Diplopoda	0.520 \pm 0.046	0.626 \pm 0.035	0.291 \pm 0.041
Amphipoda	0.036 \pm 0.015	0.999 \pm 0.001	0.752 \pm 0.043

adventive. The highest probability (0.999 \pm 0.001) that any collected Amphipoda would be an adventive was for small urban native remnants; the chances of finding an adventive species in pine were also high (Table 2).

Abundances of native Isopoda tended to be higher in native vs pine forests (Fig. 2e) ($F_{1,16} = 4.46$, $P = 0.051$), plot location and native remnant type had no effect. Oniscidae were more abundant in small urban remnants ($F_{1,16} = 7.99$, $P = 0.013$); other families were not influenced by plot location or forest type. Due to the very low number of adventive Isopoda, their abundance patterns could not be analysed statistically.

Discussion

Adventive detritivores in the forests of a modified landscape

Thirteen adventive Diplopoda species are recognised in New Zealand (Johns 2010); of these, *Cylindroiulus britannicus* and *Ophiulus pilosus* were widely distributed and abundant in our study. Both species originate from Europe and are successful invaders worldwide (Blower 1985; Mesibov 2000); in New Zealand they are widespread and common in synanthropic and disturbed habitats (Dawson 1958; Johns 1966, 1995). *Cylindroiulus britannicus* can be dominant in exotic forests (Johns 1966), and can successfully establish in native forests (Dawson 1958; Johns 1995; Ward et al. 1999), which our data confirm. *Ophiulus pilosus* was not as abundant as *C. britannicus* in our study, but more widespread. Mesibov (2000) found *O. pilosus* restricted to Europeanised habitats in Tasmania, but in our study it was found in 9 out of 10 native forests and was not restricted to smaller, more disturbed urban sites. Previously *O. pilosus* has been found in New Zealand native forests (Dawson 1958; Derraik et al. 2001), especially around the edges and along walking tracks (Johns 1995). In Waikato it was found in small forest remnants as well as in large forest reserves, and comprised 45% of all Diplopoda (Costall 2012).

Two other adventive millipedes, *Blaniulus guttulatus* and *Brachyiulus pusillus*, were less common in Manawatu-Wanganui forests despite widespread distribution in New Zealand (Johns 2010), and only occurred in small urban remnants. Our results support Mesibov (2000) who suggested that *Bl. guttulatus* and *Br. pusillus* are restricted to modified environments and do not invade less disturbed patches of native forest.

Adventive Isopoda were almost entirely absent from sampled forests. The two adventive species we found –

Armadillidium vulgare and *Porcellio scaber* – are both cosmopolitan species introduced from Europe, have been in New Zealand for over a hundred years, and are very widespread (Chilton 1909). *Armadillidium vulgare* is known to occur in native forests in New Zealand (Scott 1984; Sinclair et al. 2005). In contrast, *P. scaber* is not common in native forests (Chilton 1909), but it can sometimes penetrate considerable distances into the bush (Ward et al. 1999; Derraik et al. 2001).

Our study highlights the dominance of adventive Amphipoda in a modified landscape of the lower North Island. Adventive *Arcitalitrus* was the dominant landhopper in small native forest remnants in urban locations, and the only Amphipoda in the majority of pine forests. *Arcitalitrus* (*A. sylvaticus*) is known to be an aggressive invader; it is actively expanding its range, and is now the most common Amphipoda in modified habitats in the North Island, where it has displaced native *Puhuruhuru aotearoa* and *Parorchestia tenuis* (the two most common and widely distributed native species in the lower North Island) (Duncan 1994; Fenwick & Webber 2008). These two native species often co-occur, and appear to be less tolerant of disturbance than adventive *Arcitalitrus* (Duncan 1994). Our results suggest that native Amphipoda may be displaced by *Arcitalitrus* in native forest fragments as well, as we only found native species in sites where *Arcitalitrus* was either absent or present at low density. Absence of native Amphipoda from most pine forests and many of the native forest remnants in Manawatu-Wanganui indicates that their habitat may be limited.

Effects of remnant type and edge

There was no effect of native remnant type (small urban vs large remote) on Diplopoda and most native Isopoda in Manawatu-Wanganui. However, adventive *Arcitalitrus* landhoppers were much more abundant in smaller urban remnants. Urban development surrounding small native fragments may have facilitated the invasion of *Arcitalitrus*, as disturbance maintains the influx of adventive species from surrounding modified habitat (Didham 1997), and can cause a reversal of the competitive advantage that native species may have over adventives (Hickerson et al. 2005).

Plot location (edge vs centre) did not affect abundances of detritivores in our study. This is not uncommon, as responses of invertebrates to edge effects are site- and taxon-dependent (Didham 1997). Other studies found little impact of edge on the abundance of forest floor invertebrates in New Zealand (Norton 2002) and California (Bolger et al. 2000). Response to edges may be also masked by an interaction between confounding variables that obscure or neutralise each other (Murcia 1995; Ewers & Didham 2006). There is still much uncertainty about the scale of edge effects (Didham 1997; Ewers & Didham 2008), and it is possible that our smaller urban native remnants (< 9 ha) should be considered all edge (Bolger et al. 2000; Ewers & Didham 2008).

At the same time, the probability that any collected Amphipoda was adventive was significantly higher for edge plots. Adventive species are often more abundant at the edge of forest fragments (Harris & Burns 2000; Hickerson et al. 2005). Edges facilitate the invasion of exotic species into remaining habitat (Hickerson et al. 2005), and it is likely that, for *Arcitalitrus*, edges are key sites for invasion into forest remnants.

Pine forests as a habitat for native and adventive species

Pine plantations in New Zealand can support a number of endemic invertebrates (Hutcheson & Jones 1999; Pawson et al. 2008), and, indeed, native taxa of Diplopoda and Isopoda were as abundant in pine plantations of Manawatu-Wanganui as they were in native forests. Similarly, in Australia native millipedes were found to be as abundant and species rich in pine plantations as they were in native forests (Bonham et al. 2002; Car 2010), indicating that the native invertebrate community is involved in the breakdown and recycling of pine debris (Robson et al. 2009). At the same time, we found lower abundance of native Isopoda and a different Diplopoda community in pine forests, suggesting that some native invertebrates may be restricted to native vegetation (Samways et al. 1996; Pawson et al. 2008; Robson et al. 2009).

Higher nitrogen and other factors of litter palatability may explain higher abundance of adventive millipedes and landhoppers in native broadleaved forests compared with pine in our study. It has been demonstrated that millipedes strongly prefer litter with higher nitrogen content (Loranger-Merciris et al. 2008). Millipede *Oxidus gracilis* and landhopper *Arcitalitrus dorrieni* were found to be more abundant in broadleaved litter compared with conifer litter (Spicer & Tabel 1996; Tomlinson 2007).

A rich native understorey in pine plantations increases habitat heterogeneity and is likely to support richer invertebrate assemblages (Robson et al. 2009). Proportion and species richness of native plants in the understorey of *Pinus radiata* increases significantly with the age of the plantation (Allen et al. 1995). Presence of some native invertebrate taxa may also be facilitated by proximity to native forest remnants, as native species may disperse into adjoining pine plantations (Bonham et al. 2002; Car 2010). These factors may explain the high abundance of native detritivores (including native Amphipoda) in one of our pine forests (Kahuterawa), which at 38–41 years old is older than New Zealand's average age of pine at harvest (c. 28 years) (Pawson et al. 2008), has a diverse understorey, and lies in close proximity to a native forest.

Compared with farmland, pine forests may enhance the survival of native invertebrates (Bonham et al. 2002; Brockerhoff et al. 2005; Maunder et al. 2005). Elements of native forest fauna are able to persist in pastures if even small patches of native vegetation remain (Derraik et al. 2005). From these refugia, native decomposers are able to recolonise a pine forest planted on retired pasture. The planting of pine on intensively farmed landscapes has been proposed as an alternative to establishing native bush for the conservation of invertebrates (Mesibov 2005).

Conclusions

The temporal scale of this study allows no analysis of long-term trend, and does not account for possible seasonal and annual variations in abundance; a longer sampling may bring new dynamics. Spatially, the study is limited to native forest remnants and pine forests of Manawatu-Wanganui; we looked at small and medium-sized fragments (up to 338 ha) in a modified landscape and did not include very large tracts of native forest. However, the results are unambiguous: the study highlights a widespread presence of adventive detritivores in the forests of a modified landscape.

We hypothesised that adventive species would be more abundant in pine than in native forests, due to the resistance

of native forests to invasion, and because pine forests suffer frequent disturbance. However, adventive Amphipoda were found at similar abundance between the two forest types, and adventive Diplopoda were more abundant in native forests than in pine forests. This provides more evidence that native New Zealand forests are not resistant to invasion by adventive detritivores. The overall abundance of native Diplopoda, Isopoda, and Amphipoda did not vary between native and pine forests, indicating that pine forests may be a suitable habitat for some native taxa.

Among Diplopoda, two adventive species (*Cylindroiulus britannicus* and *Ophiulus pilosus*) were very abundant in native forest remnants, and were not restricted to smaller, more disturbed urban sites, or to pine plantations. At the same time, we found no indication that native Diplopoda were affected by human use of urban forest remnants. Native and adventive Diplopoda co-occurred, and further work is needed to identify any potential impacts of adventive Diplopoda on native species. The dominance of the adventive landhopper *Arcitalitrus* in the majority of sampled native and pine forests was unexpected, and the mechanism of the negative impact it may have on native species should be investigated.

The impact of adventive detritivores on native ecosystems and species in New Zealand forest environments has received little attention (Johns 1962; Brockerhoff et al. 2010), but worldwide there is awareness that adventive detritivores can have an unforeseen and dramatic impact on the key ecosystem processes (Frelich et al. 2006; Peltzer et al. 2010). Due to the frequency and abundance with which Julida (*C. britannicus* and *O. pilosus*) and *Arcitalitrus* were found in New Zealand native forests, their potential impact should not be ruled out. The results also highlight the urgent need for more knowledge on the taxonomy and ecology of native detritivore species.

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Supplementary Material

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

Appendix S1. Study site details.

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