



Invertebrate communities in adjacent Douglas fir and native beech forests in New Zealand

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Abstract: Non-native trees profoundly alter the structure and resilience of native forest ecosystems through direct or indirect effects on ecosystem processes, e.g. by altering invertebrate communities, but such effects are poorly understood in New Zealand. We sampled adjacent stands of the non-native tree Douglas fir (*Pseudotsuga menziesii*) and native beech (Nothofagaceae) forests and tested whether the overall invertebrate communities varied across forest types. We then assessed whether natural enemies, both trophic-generalist predators and more trophic-specialist parasitoids, differed across forest types. We found a trend for lower overall invertebrate family diversity in Douglas fir plantations compared to native beech forests. Parasitoid abundance was lower in Douglas fir forests compared to native beech forests, although we could not tease apart whether these effects were due to differences in forest age, forest type, or a combination of these factors. Our findings suggest that there are subtle shifts in invertebrate community composition from native forests to non-native forests, and that trophic specialisation might play a key role in determining which natural enemies can inhabit non-native forests in New Zealand. Nevertheless, our small sample size calls for further exploration of these patterns.

Keywords: generalist, Nothofagaceae, parasitoid, predator, *Pseudotsuga menziesii*, specialist

Introduction

The introduction of non-native trees into native ecosystems has consequences for biodiversity as well as less appreciated effects on ecosystem properties (Wardle & Peltzer 2017).

In New Zealand, the non-native tree species *Pseudotsuga menziesii* (Mirb.) Franco (hereafter Douglas fir), has been planted extensively due to its high timber value. Douglas fir, contrary to other common forestry conifer species, is relatively shade-tolerant which allows its seedlings to establish beneath native forest canopies (Cleary 1982; Ledgard 1989; Dickson 2001; Ledgard 2002; Moeller et al. 2015). There is increasing concern that Douglas fir could spread into native forests, particularly following disturbance. It is therefore important to understand the potential impacts that the increased presence of Douglas fir could have on native forest invertebrate communities and ecosystem processes.

Invertebrates play a vital role in ecological processes such as decomposition, pollination, nutrient cycling, predation, and are a major dietary component of native bird species (Evans et al. 2003; O'Donnell & Dilks 1994; Schowalter 2013). In New Zealand, some native invertebrates that inhabit forest ecosystems have adapted to commercial plantations and use them as alternative habitats. For example, Pawson et al.

(2008) found that beetle composition was similar in mature *Pinus radiata* D. Don to adjacent native forest, suggesting that non-native forests can offer additional habitats for native forest beetles in modified landscapes in New Zealand. Similarly, Peralta et al. (2018) found that *P. radiata* plantations also served as alternative habitats for some herbivorous Lepidoptera and for some parasitoid species that usually inhabit native forests. Despite these findings in *P. radiata* plantations, it remains unknown how invertebrates respond to other non-native trees such as Douglas fir, which is commonly planted throughout New Zealand. Furthermore, it is possible that invertebrate responses to large scale changes in dominant forest composition could vary depending on niche breadth or trophic specialisation (Gámez-Virués et al. 2015).

We first quantified changes in the abundance, family richness and diversity of invertebrate communities across adjacent Douglas fir and native beech forests. We then evaluated the importance of trophic generality in the response of invertebrates to changes in habitat type by focusing on natural enemy predator and parasitoid taxa within our samples. We expected that the entire invertebrate community would be more diverse in the native forest compared to the Douglas fir plantation due to higher plant diversity on native sites compared to plantations and the bottom-up effects of plants

on invertebrate communities (Peralta et al. 2018). In addition we expected that parasitoids (natural enemies with more narrow dietary requirements) would respond differently to predators (which depend on a wide range of invertebrates in their diet) to these habitat types. Specifically, we hypothesised that parasitoids would be less diverse within the Douglas fir forest because of their more restricted trophic preferences, which makes them highly dependent on specific resources, as well as their small body size, which restricts them to small effective spatial scales due to their lower dispersal abilities (Tscharrntke et al. 2004; Daoust et al. 2012).

Methods

Sampling

We selected three sites in the South Island of New Zealand: Rankleburn Forest (45°57'S, 169°25'E), Burnt Face (43°02'S, 171°38'E) and Hira Forest (41°16'S, 173°25'E). Each site consisted of native beech forest (Nothofagaceae) adjacent to mature (> 20 yrs), first rotation Douglas fir plantations (Appendix S4 in Supplementary Materials). All native beech forests contained old-growth beech trees (i.e. had not been cleared at least since European arrival) as well as other subordinate native plants such as; *Griselinia littoralis*, *Weinmania racemosa*, *Carex uncinata*, *Carex dissita* and *Lomaria discolor*. Also, in the native forest small Douglas fir seedlings (< 10cm high) were at densities averaging 6000 seedlings ha⁻¹ within 80 m of the Douglas fir plantations.

To assess differences between the invertebrate communities between native beech forest and adjacent Douglas fir forest, we sampled invertebrates using pitfall traps for a two-week period at each site between February and May 2002. At each site, twelve traps were established in three sampling locations (hereafter habitat types): (1) in the Douglas fir plantation, (2) in the native beech forest 40 m away from the last row of Douglas fir trees (hereafter Douglas fir/beech interface), and (3) in the native beech forest 120 m away from the Douglas fir plantation (hereafter beech forest) (Appendix S4). Pitfall traps consisted of plastic cups (500 ml, c. 7.5 cm diameter) that were dug into the ground and filled with a solution containing 100 ml of water and 5 ml propylene glycol solution (as a preservative). An elevated lid was placed above the trap to prevent debris and rain from filling the trap. Pitfall traps were emptied at weekly intervals. Although other sampling methods might be better suited to sample parasitoids, we used pitfall traps because they allow for the collection of a large number and wide variety of invertebrates. In addition, even if fewer parasitoids are collected using pitfall traps compared to other methods, the standardised use of trap type and sampling effort across sites and habitat types (i.e. sampling locations) allowed us to compare parasitoids among habitat types.

All adult stages of invertebrates (except for mites Acari) were identified to the family level (with the only exception of Chilopoda, identified to the class level; Appendix S1). These data of all sampled taxa were used to assess changes in family richness, abundance and diversity of all invertebrates sampled across habitat types. In addition, to assess specific changes in family richness, abundance and diversity of predators and parasitoids, we classified families with generalisable feeding habits into predators or parasitoids. Specifically, we considered families in the orders Araneae and Pseudoscorpionidae, as well as Carabidae and Chilopoda, as predators, and Hymenoptera families (Braconidae, Diapriidae,

Ichneumonidae, Pteromalidae) as parasitoids. Parasitoids are considered to be very selective of their hosts as they only attack a particular life-stage of one or several closely related host species. Data from those families that could not be classified into predators or parasitoids were considered in the analyses of all invertebrates, but excluded from the predators' and parasitoids' analyses.

Data analysis

To assess changes in the abundance, family richness (number of families) and Shannon-Wiener family diversity (index that takes into account the number of families and the evenness in abundance of each family) of invertebrates (all sampled taxa) across habitat types, we used three generalised linear mixed-effects models (GLMMs). For each model we entered the abundance, family richness or diversity of invertebrates as response variables, and used habitat type as a fixed factor with three levels (Douglas fir plantation, Douglas fir/beech forest interface and beech forest).

Likewise, to determine how the abundance, family richness and diversity of predators and parasitoids responded to different habitat types, we included the abundance, family richness and diversity of predators and of parasitoids as response variables in different GLMMs, and used habitat type as a fixed factor in all the models. We included site as a random factor in all the models. For the abundance and family richness models we used a Poisson error distribution, and for the diversity models we used a Gaussian error distribution. We tested their corresponding assumptions (overdispersion of residuals in the Poisson models and normality and homoscedasticity in the Gaussian models) and used a negative binomial distribution when the equidispersion assumption of the Poisson model was not achieved (Zuur et al. 2009). All linear model analyses were performed in the R environment (R Core Team 2019). We used the `glmer` and `glmer.nb` functions from the `lme4` package (Bates et al. 2015) for the Poisson and negative binomial models, respectively, and the `lmer` function from the `lmerTest` package (Kuznetsova et al. 2017) for the Gaussian models.

Results

Overall, we collected 2435 invertebrates from 55 families (Appendix S1), with the highest richness (28 families) recorded at the Douglas fir/beech interface at the Burnt Face site and in the beech forest at the Hira Forest site. When analysing all the invertebrate taxa together, despite a trend of lower family richness and diversity across all taxa in Douglas fir plantations compared to the Douglas fir/beech interface and beech forest, there were no significant differences (Fig. 1; Appendix S2).

Similarly, we did not observe differences in the abundance, richness or diversity of predators between Douglas fir plantations, Douglas fir/beech forest interface or beech forest (Fig. 1; Appendices S3, S5). Conversely, the abundance of parasitoids was significantly higher in both beech forest habitat types (i.e. in the Douglas fir/beech forest interface and the beech forest) compared to the abundance of parasitoids in Douglas fir plantations. This difference in the abundance of parasitoids between habitat types was mostly driven by the high abundance of Braconidae in beech forest, but also by the absence of Ichneumonidae, Pteromalidae and Diapriidae from the Douglas fir forest (Appendix S5). Finally, there were no differences in family richness and diversity of parasitoids across the three forest types (Fig. 1, Appendix S3).

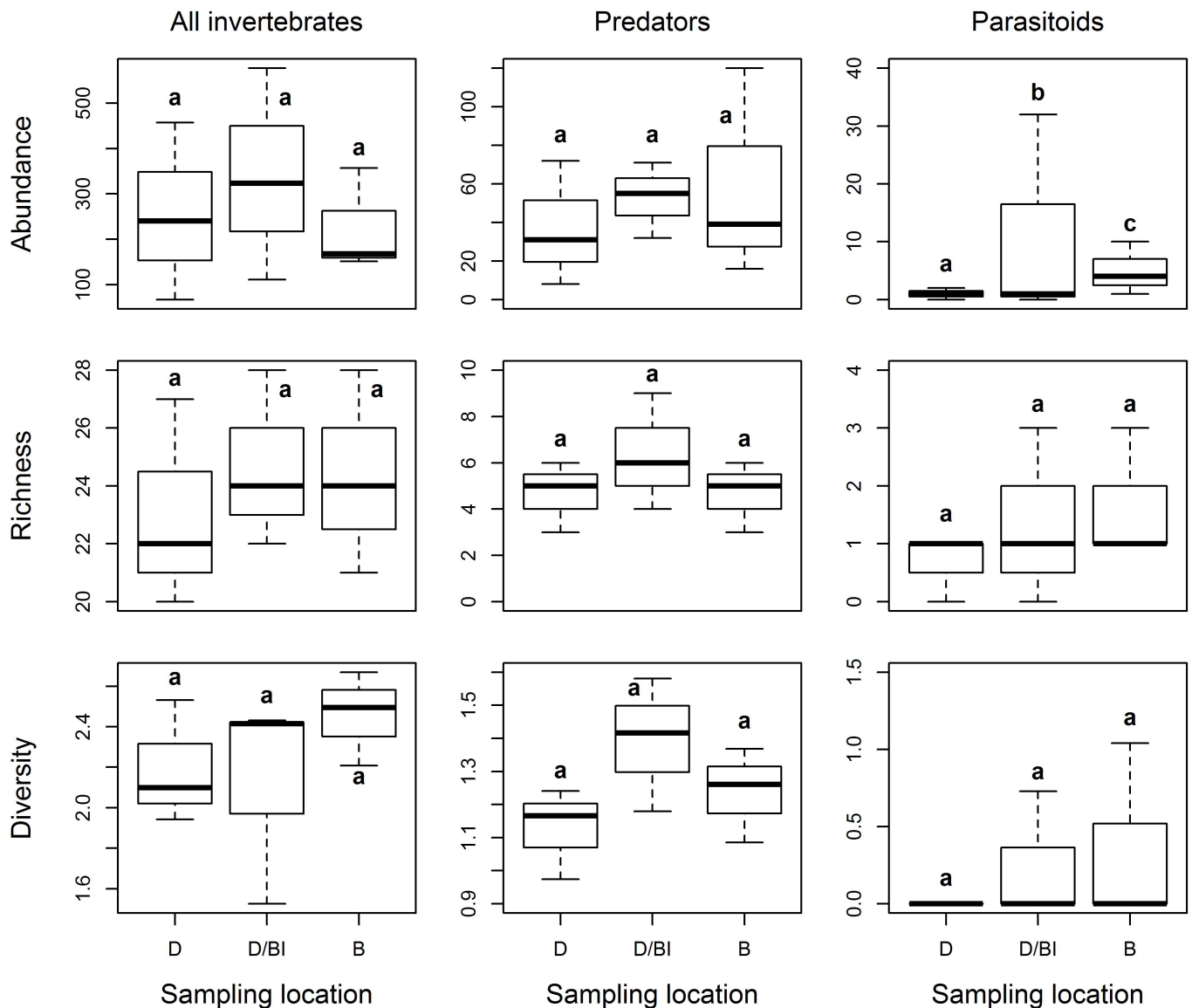


Figure 1. Abundance, family richness (number of families) and Shannon-Wiener family diversity of all invertebrates, predators and parasitoids across habitat types: D = Douglas fir forest; D/BI = Douglas fir/beech interface; B = beech forest. Different letters on bars indicate significant differences ($P < 0.05$).

Discussion

Contrary to our prediction that total invertebrate diversity would be highest in native beech forests, there were no consistent differences in overall invertebrate abundance, family richness or diversity among Douglas fir plantations, the Douglas fir/beech interface and beech forest. However, the abundance of parasitoids was significantly lower in the Douglas fir plantations compared with the Douglas fir/beech forest interface and beech forest habitats.

The higher abundance of parasitoids in native beech forests compared to Douglas fir plantations, could reflect the simplified plant composition in the plantation which could translate in the lack of suitable resources for parasitoids available in the non-native environment. Our results suggest a subtle change towards a more homogenous invertebrate community dominated by generalist species that are better able to adapt to local conditions, but we acknowledge that our conclusions

are based on a small sample size. Because trophic generalist species can make dietary adjustments to different conditions, they are typically more resilient than specialist species, such as parasitoids. Although theory indicates communities composed of more resilient species could be more resilient to future changes, this comes with the cost of losing diversity which is critical for the stability of ecosystem functions (Yachi & Loreau 1999; Gámez-Virués et al. 2015).

There were no significant differences in abundance, diversity and richness of families across all taxa (or when looking at predators only) between Douglas fir plantations and native beech forests. It is possible that as Douglas fir plantations age, the composition of invertebrate communities sampled with pitfall traps becomes increasingly similar to that of native beech forests due to an increased number of native plants colonising the plantation understory. Therefore, old Douglas fir plantations could represent alternative habitats for at least some invertebrates, as found for other pine plantations

in New Zealand (Pawson et al. 2008; Peralta et al. 2018). Nevertheless, considering the commercial interest of Douglas fir plantations, the potential of Douglas fir to expand beyond the plantation limits (i.e. invade native forests), and given the low power in our analyses (three sites sampled may be insufficient to detect small effect sizes), we encourage future research to further evaluate changes in diversity across these forest types using a larger number of study sites and a more diverse set of sampling methods (e.g. including traps specifically design for collecting flying insects). In addition, future research should attempt to tease apart the influence of forest type vs forest age on invertebrate communities. To this end, future studies could compare invertebrate communities from Douglas fir plantations of different forest ages vs regenerating native forests of different ages.

The maintenance of functionally diverse invertebrate communities should be prioritised and considered in the context of retaining New Zealand's highly endemic flora and fauna. Greater attention is needed to understand the consequences of vegetation changes for biological communities such as those associated with commercial plantations, pastures and plant invasions. Specific attention needs to be placed on the effects of plant species used commercially (particularly those with tendencies to invade native ecosystems such as Douglas fir), at least until new technologies such as the use of sterile trees becomes available. In summary, our findings support previous studies indicating that non-native plantation forests can provide habitat for a subset of native invertebrates (Brockerhoff et al. 2001; Brockerhoff et al. 2005; Pawson et al. 2008), but also highlights that gradual changes in the dominant tree species found in New Zealand's native forests could have negative implications for the composition of forest-dwelling invertebrates.

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Author Contributions

AME: obtained and administered the funding, designed the study, supervised the field work, assisted with the identification of invertebrates and writing/review/editing of manuscript. GP: statistical analysis, writing/review/editing of manuscript. FVB: involved with collection of the data, assisted with invertebrate identification, writing/review/editing of manuscript. KK: involved with collection of the data, assisted with invertebrate identification, writing/review/editing of manuscript. DAP: writing/review/editing of 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 abundance for each invertebrate family observed for all combinations of study site and habitat type.

Appendix S2. Coefficients of three generalized linear mixed-effects models used to determine changes in the abundance, richness (number of families) and diversity (Shannon-Wiener family diversity) of invertebrates across habitat types (Douglas fir plantation, Douglas fir/beech forest interface, beech forest).

Appendix S3. Coefficients of six generalized linear mixed-effects models used to determine changes in the abundance, family richness (number of families) and Shannon-Wiener family diversity of predators and parasitoids across habitat types (Douglas fir plantation, Douglas fir/beech interface, beech forest).

Appendix S4. Schematic diagram of each sampling site. Each site (three sites in total sampled across the South Island of New Zealand) comprised a Douglas fir plantation adjacent to a native beech forest.

Appendix S5. Abundance of predator and parasitoid taxa across habitat types.

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