Interactions between indigenous southern Afrotemperate forest trees and arthropod diversity

by

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Declaration

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General summary

Although small compared to other temperate rainforests in the southern Hemisphere, the southern Cape Afrotemperate forest complex is the largest in South Africa. While it occurs at temperate latitudes, it has strong tropical elements resulting from its paleo-history. Of the numerous species occupying forest ecosystems, insects comprise a major part of the total biodiversity, most of which occur in tree canopies. Prior to this study, little work had been done on insects in southern Afrotemperate forests in general, and no work at all has been done on the diversity and distribution of their canopy-inhabiting arthropods. Therefore, the aim here is to determine the extent to which various environmental factors affect the interaction between indigenous tree species and associated arthropod diversity in South African Afrotemperate forests.

I first determine whether the context and contrast in which an individual tree grows (i.e. where it grows and what surrounds it) will impact its physiology and associated canopy arthropod diversity. I found that the contrast of vegetation surrounding an individual tree can affect leaf morphology, and, in turn, its ability to host particular arthropods, with trees with low contrast (i.e. surrounded by denser vegetation) revealing larger leaves and increased arthropod diversity. Furthermore, plant physiological features fluctuated according to the context in which a tree grows (natural, semi-natural, or planted vegetation), which affected associated canopy arthropods. Therefore, to optimally conserve local arthropod diversity using indigenous tree plantings in transformed landscapes, it is imperative to mimic natural tree context and natural variations in contrast.

Forest arthropods maintain ecosystem health by driving ecosystem processes such as litter decomposition. I designed an experiment to compare the litter decomposition performed by arthropods vs. fungi, and determined which local factors influence variations in decomposition rates. In addition, I tested the home-field advantage (HFA) hypothesis at the tree-level. The HFA states that leaf litter decomposes more rapidly beneath plant species from which the leaves originate (home environment), than under other plant species. I demonstrated that arthropods perform the bulk of the decomposition function in these forests, and that their ability to do so varies significantly between different tree species,

although the role of bacteria may also be substantial. Contrary to expectations, and despite selective arthropod responses toward different source leaves, HFA is not prevalent in this mixed forest system.

Given the responses of arthropods to tree identity, tree context- and-contrast, and accompanying changes in plant physiological features, it was reasonable to assume that these factors may influence arthropods associated with the canopies of southern Afrotemperate forests. I therefore established the relative effects of tree species identity, plot characteristics, and plant physiology on the diversity and distribution of canopy arthropods. Tree species identity and differences in plant physiological features explained differences in arthropod diversity between individual trees. Individual trees surrounded by denser vegetation also had less diverse arthropod assemblages compared to trees in more open areas. I argue that in diverse mixed forests, tree crown heterogeneity is of significant importance in conserving arthropod diversity, driven not only by architectural variation, but also by fluctuating levels of light exposure. Differences in plant physiological features at the tree species level was accompanied by many effects on canopy arthropods, which would make generalisations of forest arthropod responses to anthropogenic changes difficult.

As this study represents a first attempt to describe the diversity of arthropods in the canopies of southern Afrotemperate forests, I conclude by providing a synthesis of this diversity, placing it in a global context. I provide evidence that arthropod diversity in these forests is more similar to those of temperate forests than to arthropods associated with tree canopies in tropical forests. However, these forest canopies are ten-fold richer in species than the forest floors in this region. Combined with the high numbers of species sampled, many of which are undescribed, special conservation efforts is justified to protect southern Afrotemperate forest canopies across a wide biogeographical gradient.

Algemene opsomming

Ten spyte daarvan dat die suidelike Afro-gematigde woudkompleks klein is in vergelyking met ander gematigde woude in die suidelike halfrond, vorm dit die grootse woudkompleks in Suid-Afrika. Vanweë die unieke paleo-geskiedenis van die area, het die woude egter ‘n tropiese affiniteit. Van al die verskeie spesies wat woud-ekosisteme bewoon, is insekte ‘n groot deel van die totale biodiversiteit, en die meeste hiervan kan in boomtoppe gevind word. Voor hierdie studie, is baie min fokus geplaas op insekte in suidelike Afro-gematigde woude in die algemeen, en geen studie het gepoog om die diversiteit en verspreiding van boomtop-insekte te beskryf nie. Die doel van hierdie navorsing, dus, is om te bepaal tot watter mate verskeie faktore die interaksies tussen inheemse boomspesies en geassosieërde arthropoda diversiteit affekteer in Suid-Afrikaanse Afro-gematigde woude.

Eerstens het ek bepaal of die konteks en kontras waarin ‘n individuele boom groei, die fisiologie en geassosieërde arthropoda sal beïnvloed. Ek het bevind dat die kontras van die omringende plantegroei rondom ‘n boom die blaarmorfologie en gevolglik die arthropoda beïnvloed, met bome in laer kontraste (omring deur digter vegetasie) wat groter blare en verhoogde diversiteit getoon het. Plant fisiologie het gefluktueer op grond van die konteks waarin ‘n boom groei (natuurlik, semi-natuurlik, geplant), wat geassosieërde boomtop arthropoda geaffekteer het. Om plaaslike arthropoda optimaal te bewaar deur inheemse bome te plant, is dit daarom van kardinale belang om ‘n boom se natuurlike konteks en variasie in kontras in ag te neem.

Woud arthropoda onderhou gesonde ekosisteme deur ekosisteem prosesse soos blaar dekomposisie te dryf. Ek het ‘n eksperiment ontwerp om die blaar dekomposisie wat uitgevoer word deur arthropoda teenoor fungi te vergelyk, en om te bepaal watter plaaslike faktore die variasies in dekomposisie tempo sal affekteer. Verder, het ek die tuisveld-voordeel (TVV) hipotese getoets, wat stel dat blare vinniger afbreek onder plante vanwaar die blare afkomstig is (tuis), teenoor ander plant spesies (weg). Hier demonstreer ek dat arthropoda die meeste dekomposisie funksie uitvoer, en dat hul vermoë om dit te doen beduidend varieër tussen verskillende boomspesies, alhoewel die rol van bakterieë substansieël

mag wees. Anders as verwag, en ten spyte van selektiewe arthropoda reaksies tot verskillende boom-spesie blare, blyk TVV nie van belang te wees in hierdie gemengde woudsisteem nie.

Gegewe die reaksies van woudvloer arthropoda tot boom identiteit, boom konteks- and kontras, en gepaardgaande veranderinge in plant fisiologie, is dit redelik om te verwag dat hierdie faktore die boomtop arthropoda in suidelike Afro-gematigde woude kan beïnvloed. Daarom het ek die relatiewe effekte van boomspesie-identiteit, plot eienskappe en plant fisiologie op die diversitiet en verspreiding van boomtop arthropoda bepaal. Boomspesie-identiteit en verskille in plant fisiologie het verskille in arthropoda diversiteit tussen individuele bome bepaal. Individuele bome omring deur digter plantegroei het minder diverse arthopoda samestellings gehad in vergelyking met meer oop areas. Ek argumenteer dat, in diverse, gemengde woude, heterogene boomtop lae van beduidende belang is om arthropoda diversiteit te bewaar, gedryf nie net deur variasie in argitektuur nie, maar ook deur fluktuasies in lig blootstelling. Verskille in plant fisiologie by die boomspesie-vlak het gepaardgegaan met ‘n diverse verskeidenheid effekte op boomtop arthropoda, wat algemene afleidings van hul reaksies tot mensgedrewe veranderinge bemoeilik.

Aangesien hierdie studie ‘n eerste poging is om die diversiteit van arthropoda in boomtoppe van suidelike Afro-gematigde woude te beskryf, sluit ek dit af deur ‘n volledige sintese te verskaf van hierdie diversiteit, en om dit in ‘n globale konteks te plaas. Ek verskaf bewyse dat arthropoda diversiteit in hierdie woude meer soortgelyk is aan ander gematigde woude s’n, meer so as in vergelyking met tropiese woude. Tog het boomtoppe in hierdie area ‘n tien-maal hoër spesies rykheid as woudvloere in dieselfde area. Indien dit gekombineer word met die hoë aantal spesies wat versamel is, meeste waarskynlik onbeskryf, regverdig dit spesiale bewaringspogings om suidelike Afro-gematige woude se boomtoppe oor ‘n wye biogeografiese gradiënt te beskerm.

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Contents

Chapter 1: General Introduction and Research Aim

Forests of the world

Forests form part of living nature's largest manifestations. In forest ecosystems, trees are dominant features, creating many micro-climates and modifying life conditions below elevated greenery. Apart from emergent trees, natural forests are also home to shrubs, small trees, graminoids, herbaceous plants, ferns, vines, climbers and epiphytes. This complex and structurally diverse floral environment allows for a great variety of fauna to develop, leading to massive numbers of interactions between numerous species. Indeed, our most diverse ecosystems are natural forests, specifically those occurring in the tropics. Globally, Asia has by far the largest percentage (31%) of forest cover of all continents, including the Boreal forests of Russia and the subtropical to tropical, very threatened forests of Southeast Asia. This is followed by South America (21%), Africa (17%), North and Central America (17%), Europe (9%) and Oceania (5%) (FAO 2010). Today, 30% of the earth's surface is covered by forests, 5% thereof being plantations (FAO 2010; Pan *et al*. 2013). Despite covering less than a third of the earth's surface, forests contain 80% of the world's total plant biomass (Kindermann *et al*. 2008). Three of the world's five *high biodiversity wilderness areas* are forests: The Amazon, the Congo and the forests of New Guinea. Together, these three bio-diverse regions holds more than 65 000 vascular plant species, 1000 mammalian species and more than 2500 bird species, still counting (Mittermeier *et al*. 2003). Its insect fauna, as recently argued, goes well into the millions (Stork 2018), creating the most biodiverse regions on the planet. Apart from the hyper-diverse tropical forests around the equator, moving north we find the vast Boreal forests, hosting more than 2000 vascular plant species, 200 mammalian species and 650 or so species of bird. These forests, having gone through long periods of glaciation, especially during the Quaternary period (Davis 1983), are no less splendorous due to its sheer size (approximately 16 000 000 km^2) and remoteness (80% intact) (FAO 2010). Evidently, without forests, the diversity of life on earth would be a fraction of what we see today.

Temperate rainforests

Further south of the equator occurs the scarce southern temperate rainforests of the world. These are areas receiving high rainfall occurring in the southern hemispheric, temperate zones of the earth. These forests include, among others, the Valdivian and Magellanic forest complexes of southern South America, the temperate rainforests of Australia and Tasmania and the New Zealand temperate rainforests. Temperate rainforests, even though not as species rich as their tropical counterparts, or as extensive as the Boreal forests, are among the densest and tallest forests (Pan *et al*. 2013). They occupy a small percentage of temperate regions, and usually grow near oceans and coastal mountains. Besides receiving high precipitation (more than 800-1000 mm p.a., Lee *et al*. 2016) and occuring in temperate zones across the globe, they do not necessarily share a common origin. However, in many forests in the southern hemisphere, including the forests of southern South America, New Caledonia, New Zealand, Australia, Tasmania, and to a lesser extent southern South Africa, a strong Austral floristic component occurs, hinting at a once shared geographical location now divided (McGlone *et al*. 2016). The similarities in physiognomy and shared key taxa between these forests have been noted from as early as the 1850's (Hooker 1853; Darwin 1859). These similarities indicate a once connected forest ecosystem stretching across the southern continent of Gondwana, with some work suggesting that Antarctica was, during the Cretaceous, a region of origin and dispersal for many elements of today's southern hemispheric forests (Dettmann 1989). New Zealand and southern South America, together with Australia and Tasmania, have received much attention because of similarities between lineages (Kooyman *et al*. 2014), such the close relation between *Podocarpus nubigenus* of Valdivian temperate rainforests and *P. totara* endemic to New-Zealand (Simpson 2017), separated by >8000 km of open ocean. Today, the Gondwanan forest lineages, having speciated *in situ* in their respective novel habitats over millennia, make up significant components of the present southern temperate rainforests and usually co-occur with other, widely-separated lineages to form unique forest communities (Kooyman *et al*. 2014). A good example is the remaining forests of South Africa, which today have taxa of Gondwanan origin persisting in forests which have strong subtropical and tropical affinity.

Southern Afrotemperate forest complex

Most of South Africa is extremely dry and unable to support forest establishment and growth. However, from the Cape Peninsula in the extreme southwest and following the major mountain ranges towards the Eastern Cape, and then extending north-eastwards through KwaZulu-Natal, the Eastern Free State and Mpumalanga, and even farther north towards the Soutpansberg Mountain range in the Limpopo province, there is a great variety of forest communities. In total, it is estimated that about 20 000 forest patches occur in South Africa, comprising a suggested eight forest groups, subdivided into 32 forest types (Berliner 2009). Perhaps the smallest, but nevertheless interesting examples of temperate rainforests on the globe, are the forests forming part of the Knysna-Amatole coastal complex at the southern tip of South Africa. Although small compared to other temperate rainforests in the southern Hemisphere, the southern Cape forest complex is the largest in South Africa and, although having a temperate location, has a conspicuous tropical affinity. However, before tropical elements became major contributors to these forests, ancient Gondwanan lineages were present in the present-day south-western Cape, and many lineages still thrive despite numerous historic climatic regime shifts and isolation from other southern land masses.

Origin of southern Afrotemperate forests

During the Palaeocene (55-65 my BP), the southern tip of Africa is speculated to have been covered by mostly temperate forests, mostly of Gondwanan origin (Axelrod & Raven 1978; Deacon 1983). By this time, Gondwana had already broken up (Burke & Gunnel 2008). Temperate lineages that were represented in this era, and are still present today, include among others the genera *Widdringtonia*, *Podocarpus*, *Cunonia* and *Platylophus* (Von Breitenbach 1974). Subtropical and tropical forests, during favourable climatic conditions in the Oligocene-Miocene, became dominant features of the south-western Cape by moving southward from continental Africa along river valleys and coastal plains, penetrating the original southern flora (Von Breitenbach 1974; Axelrod & Raven 1978; Deacon 1983). Whereas *Podocarpus latifolius* (Real Yellowwood) and the closely related *Afrocarpus falcatus*

(Outeniqua Yellowwood), of temperate origin, became dominant features of these novel forests, lineages such as *Widdringtonia* in the south Western Cape for example, did not adapt to these mostly tropical forest communities and became restricted to mountainous shrublands and the outskirts of forests (Von Breitenbach 1974). Also, genera such as *Podocarpus* had relative success in these novel habitats, expanding northward and reaching Kenya around 25 my BP (Vincens *et al*. 2006; Galley *et al*. 2006). *Cunonia capensis*, the only species of the genus *Cunonia* occurring outside of New Caledonia, where 25 endemics occur (Pillon et al. 2008), again survived these floral shifts through adaptation, and today occur mostly close to water or forest edges in the southern Afrotemperate forests, while becoming dominant elements of many smaller natural Western Cape Afrotemperate forest patches (Von Breitenbach 1974).

Despite the presence of temperate elements, lowland and montane subtropical rainforest, with palms being prominent, characterised the Oligocene-Miocene era (Coetzee 1978; 1983). At present, this vegetation type is absent, although the southern Cape Afrotemperate forest complex is considered as impoverished remnants (Coetzee 1978; 1983). Tropical lineages today are featured in both the southern Cape forests, and tropical Africa (Von Breitenbach 1974). Southern Cape forests also contain genera endemic to the Afromontane Archipelago, such as *Olinia*, regarded as a western Gondwanan clade, and *Trichocladus*, a genus native to South Africa and Zimbabwe (Endress 1989; Sebola & Balkwill 2013).

Overall, there is a distinct decline in forest floral diversity moving east to west in South Africa, as many species migrating south either never reached the extreme south-western parts of the Cape, or have since retracted their distribution in accordance with climatic changes (Von Breitenbach 1974). Indeed, this pattern is seen for many woody species even in the small strip of land between Table Mountain and Tsitsikamma. *Brachylaena glabra*, commonly referred to as the Malabar tree, does not occur further west than the forests of Storms River in the Eastern Cape. *Canthium pauciflorum* does not occur across the Keurbooms River near Plettenberg Bay, Western Cape. *Ochna natalitia* distribution ends west of the Knysna forests, whereas common species such as *Ficus capensis*, *Maytenus peduncularis, Ochna arborea, Trimeria grandifolia* and *Dovyalis rhamnoides* only occur east of George (Von Breitenbach

1974). In summary, many genera of tropical origin today are prominent components of southern Afrotemperate forests, and together with southern lineages, make up the bulk of southern Afrotemperate forests. Indeed, there are similarities in genera between the Cape and areas as far north as Ethiopia following the major mountain massifs, and has been of interest for botanists for more than 150 years (Grimshaw 2001). Also, the similarities between southern hemisphere temperate rainforests in general, including the southern Cape forests, are equally striking.

Fynbos and arid shrublands today are the dominant vegetation in the south-western Cape, and are believed to have become dominant during the late Pleistocene (125 000 – 10 000 y BP) after having diversified rapidly during the late Miocene (Geldenhuys 1997; Mucina & Geldenhuys 2006). This is a result of the cold Benguela current, which at about 23-16 My BP gradually strengthened due to, predictably, the opening up of the Drake Passage (± 49-17 my BP; Scher & Martin 2006) between South America and Antarctica (Neumann & Bamford 2015). Since the beginning of the Miocene, the south-western Cape vegetation experienced the effect of the cool Benguela current which led to winter rainfall and semi-arid conditions (Deacon 1983). Predictably, inland forest patches of the south-western Cape became increasingly isolated as a result of this aridity (Geldenhuys 1997). During the late Miocene and Pliocene, fire-prone vegetation experienced ‘fast diversification and a maximum radiation of its clades’; suggesting that forest expansion would have, during this era, been controlled by fire along with drier limiting conditions (Mucina & Geldenhuys 2006; Neumann & Bamford 2015). Today these forests occupy a fraction of the natural landscape. Forests form the smallest biome in the country, with only about 0.56% of land surface area covered by indigenous, evergreen forests (Low & Rebelo 1996). The discontinuity of the forest biome we witness today is therefore a result of historic climatic fluctuations and natural disturbance regimes, especially during the last 180 000 years (Partridge *et al*. 1999; Eeley *et al*. 1999; Lawes *et al*. 2000). Indeed, forest patches are rarely larger than 1 km² and are essentially islands each of distinct floristic composition amidst differing, lower growing vegetation communities surrounding them (Eeley *et al*. 1999, 2001). However, even with its small size and fragmented nature, these forests contain much biodiversity worthy of conserving (Geldenhuys 1989).

In summary, the tropical origin of the southern Afrotemperate forests explains their current composition. However, due to relict southern floral elements, these communities are not wholly tropical (Von Breitenbach 1974). Today they comprise a combination of floral elements from subtropical, tropical, and temperate origins, reflecting the major floristic and climatic shifts that have occurred at the southern tip of South Africa, the continent, and the southern hemisphere as a whole. Tree individuals are mostly part of a community, and associated with them is much other biodiversity that is fully or at least partly dependent on their presence, health, and continuance.

Exploring the forest canopy

Of the numerous species occurring within forest ecosystems, insects comprise a large part of the total biodiversity. Erwin (1982) first suggested that there had previously been a major underestimation of global biodiversity after his novel work on canopy arthropod diversity in the tropical forests of Panama. From his conservative estimates on insect diversity, he concluded that there could be 41 389 species per hectare of scrubby seasonal forest in Panama. He went even further to suggest that there might be up to 30 million species of tropical arthropods! Although these figures are only estimates and have since been challenged (e.g. Stork 2018), they do suggest that prior to 1982, we greatly underestimated the richness of global biodiversity.

Since there has been much more work on forest canopies (e.g. Moran & Southwood 1982; Stork 1987; Reynolds & Crossley 1997). We now know that major consumers in forests are herbivorous insects (Novotny & Basset 2005). Moreover, it is estimated that about 40% of extant terrestrial species occur within the forest canopy (Price 2002; Novotny & Basset 2005), contributing greatly towards local and large-scale ecosystem functioning. Herbivorous insects, as a group, contribute greatly towards the high level of biodiversity found in forest canopies (Price 2002) and, as a result, we consider the interactions between herbivorous insects and their tree hosts as vitally important, and our understanding of them even more so. From the highly diverse, sunlit forest canopy down towards the damp, shaded forest floor, insects have colonised almost every available micro-habitat. Their role in maintaining forest ecosystems is unmatched compared to other animals, whether through herbivory, saproxyly, or pollination, and interactions ranging from antagonistic to mutualistic.

Insects in trees – regional differences

In terms of plant diversity, plant species richness reaches its peak near the equator (Novotny *et al*. 2006) with plant species richness being up to six times higher per hectare in the tropics compared to temperate forests (Novotny *et al*. 2006). Whether or not insects follow similar patterns remains poorly understood, but canopy sampling is helping improve knowledge.

Novotny *et al*. (2006) concluded after comparing temperate and tropical tree host specificity for herbivorous insects, that no differences exist in herbivore-tree host specificity between the tropics and temperate zones, and that differences in insect species richness between these regions are driven more by plant species richness patterns. However, they did acknowledge that differences in specialization exists for different insect groups between the two regions, with for example, the Papilionidae being more specialized in the tropics compared to Lycaenidae: Polyommatini, which are more specialized in temperate regions (Scriber 1988). Other groups for which known differences occur are the bark beetles (Curculionidae: Scolytinae), and also treehoppers (Hemiptera: Membracidae), which are seemingly more specialized in temperate areas (Beaver 1979; Wood 1984).

Ants are a particularly interesting canopy group, with great differences between tropical and temperate trees. Temperate trees have between 0.2 – 3 % ant abundance as a total of canopy catches (Moran & Southwood 1982), compared to 18 - 53 % for tropical trees (Moran & Southwood 1982; Erwin 1983; Adis *et al*. 1984; Stork 1987). From tropical Borneo, Stork (1988) found ants to dominate sampled abundance (± 18 %). However, ant species were represented by only 99 out of a total of 2 800 species (< 5 %). About 5 000 km southeast, canopy fogging of the Australian subtropical tree *Argyrodendron actinophyllum*, revealed only 2 % ant abundance placing it closer to temperate trees (Basset 1991). One hypothesis is that arboreal ants in temperate areas may be limited by seasonal variation in productivity (Majer 1990), a hypothesis supported by the findings of Basset (1991). The high abundance and biomass of spiders could indicate that spiders have taken over predatory roles from ants in temperate areas (Basset 1991), as this group is more resilient to seasonal limitations (Reichert & Harp 1987).

Another interesting group is the rest of the Hymenoptera (i.e. non-Formicidae). In a Bornean canopy study, non-Formicidae Hymenoptera were the most species-rich group, followed by Coleoptera and Diptera (Stork 1988). About 1455 chalcidoid wasps (6 % of total abundance) were sampled, comprising a massive 739 species (> 26 % of total species richness). Of this hyper-diverse group, 437 species were sampled as singletons (Stork 1988). The abundance of non-Formicidae Hymenoptera is in line with other studies from the tropics, for example from Central Amazonia (6 % of total numbers; Adis *et al*. 1998) and the Pantanal (4 % of total numbers; Marques *et al*. 2006).

The Coleoptera is arguably the best studied arthropod group in tree canopies, and also one of the most diverse. Between tropical and temperate sites, and between sites within these regions, there are great differences in the diversity of beetles. For instance, Alison *et al*. (1997) found a total of 418 beetle species from eight trees of a single species, *Castanopsis acuminatissima*, from tropical New Guinea (mean = 144 beetle spp. per tree). Here, the most abundant beetle families were (from highest to lowest): Chrysomelidae, Staphylinidae and Curculionidae. Erwin (1983) concluded from Manaus, Central Amazonia, that the top five species-rich families of beetle were Curculionidae, Chrysomelidae, Tenebrionidae, Coccinellidae and Cerambycidae in descending order. In Panama, Erwin & Scott (1980) found the most species rich beetle families from a single tree species, *Leuhea seemmani*, to be Chrysomelidae, Staphylinidae, Cerambycidae, Mordelidae and Carabidae, compared to Brunei, where from five tree species, the most species rich beetle families were Curculionidae, Staphylinidae, Chrysomelidae, Aderidae and Anthribidae (Stork 1991). From the subtropics, in a forest near Brisbane, fogging of the tree species *A. actinophyllum* showed the most dominant coleopteran families to be, from highest to lowest: Chrysomelidae, Scolytidae, Corylophidae, Staphylinidae and Curculionidae (Basset 1991). Another study, from the temperate rainforests in Chile which focused on Gondwanan lineages only, found nearly 500 beetle species, the most abundant and species rich family being Curculionidae (Arias *et al*. 2008). Regardless of much divergence between taxa found, the most represented beetle families largely seem to include Chrysomelidae, Staphylinidae and Curculionidae. Also, it is clear that there are large differences between tropical and temperate trees.

Roles of insects in forests

Insects exhibit not only great variety in their taxonomy, but also in the way they feed. Whereas there are large variations in classifying insect herbivores according to their guilds (Cornell & Kahn 1989), a comprehensive guild classification was described by Novotny *et al*. (2010). Initially suggesting 72 possible guilds for herbivorous insects, eventually this number was lowered to 24. Insect herbivores are placed into guilds based on an array of characteristics, e.g. leaf sucking, leaf chewing, leaf mining, phloem sucking, xylem chewing etc. Insect herbivory is, evidently, not restricted to leaves of green plants only, but encompass a wide range of niches within their respective habitats. Although the interactions between herbivorous insects and plant hosts account for much of terrestrial biodiversity, many species at higher trophic levels also depend on insect herbivores as food sources (Price *et al*. 1980). This highlights the central role of insect herbivores in maintaining complex ecosystems like forests. Recent work has shown that herbivorous insects could even significantly limit the capacity of forests to act as carbon sinks (Couture *et al*. 2016). Their functional importance therefore stretches far wider than only at the local- or regional scale, highlighting the significant ecological role of such a species-rich group.

While insect herbivores are abundant in forest canopies and contribute significantly towards ecological functioning and diversity within the forest canopy, they also play important roles in the lower layers of the forest. Hunter *et al*. (2003), for example, suggested that canopy herbivores influence forest soil processes, but with strong spatial and temporal components. Hunter (2001) lists seven ways in which this is possible. Firstly, herbivores alter soil nutrients through deposition of herbivore faeces into the soil. Secondly, they do so through inputs into the soil by insect cadavers. The third way is by changing the chemistry of precipitation, or through fall *via* defoliator-mediated means. Fourthly, herbivorous insects alter the quality and quantity of litter inputs from the forest canopy. Fifthly, they change the nutrient uptake by plant communities. Sixthly, they could impact root/mutualists interactions, and lastly, they exhibit effects upon the physical structure of plant canopies and indirectly facilitate subsequent changes in the soil microclimate (from Hunter, 2001). The impact of such a functionally diverse and species-rich group as forest canopy herbivores consequently stretches across the different forest strata.

Recent work further suggests that herbivory at the above-ground level, i.e. the forest canopy could markedly influence not only soil properties, but even the eventual leaf litter decomposition process (Grime *et al*. 1996; Wardle *et al*. 2004; van Dam & Heil 2011; Couture *et al*. 2016). The decomposition of leaf litter in forests returns nutrients from organic material back into the soil, with plant productivity strongly depending on this process (Gartner & Cardon 2004). This is one of the most important processes affecting nutrient cycling and forest productivity (Cuevas & Medina 1988; Didham 1998). Soil and leaf litter arthropods, together with microbes, play significant roles in leaf litter decomposition (Seastedt 1984; Seastedt & Crossley 1984, 1988), and are known to be greatly affected, as most arthropods are, by the micro-climate of a given location (Bokhorst & Wardle 2013; Cuke & Srivastava 2016). Further factors known to affect leaf litter decomposition include climate itself (Shanks & Olsen 1961; Aerts 1997), micro-environment surrounding the litter (Hornsby *et al.* 1995), chemical composition of the litter (Pereira *et al*. 1998; Lill & Marquis 2001) and the structure of the decomposer community (Seastedt & Crossley 1984; Zak *et al*. 1990). Another factor is the species composition of litter, with research suggesting the species to have a significant effect on the rate of leaf litter breakdown (Shanks & Olsen 1961). Other work even suggests that the species of tree has a greater effect on leaf litter breakdown than rainfall (Wieder *et al*. 2009; Dale *et al*. 2015).

Soil communities tend to specialize on the plant species above it (Ayres *et al*. 2009; Strickland *et al*. 2009). These observations support previous work, suggesting that home-field advantage (HFA) greatly contributes to the eventual leaf litter breakdown process (Bocock *et al*. 1960; Hunt *et al*. 1988; Vivanco & Austin 2008). HFA states that leaf litter decomposes more rapidly underneath species from which it originates than from other species (Gholz *et al*. 2000). One reason put forward to explain this phenomenon is the local adaptation of the soil community, which through specializing locally, gains faster access to energy and nutrients contained within the leaf litter (Ayres *et al*. 2009). It is quite possible that resource use by macro- and micro-invertebrate decomposers could be species specific, and that such species are wholly dependent on a single species of host tree and, in the light of HFA, even dependent on a certain location within a larger community (i.e. underneath its host tree). However, HFA is still poorly understood at the level of individual trees. HFA in essence supports (for detritivores) the resource concentration hypothesis, stating that herbivorous insects are 'less likely to find and remain in patches in which their host plant is less likely to be encountered' (Castagneyrol *et al*. 2014). Viewing trees as creators of micro-habitats and, for the very small, even a 'patch' in its own right, we can expect to find at least some levels of specificity between a host tree's leaf litter and micro- and even macro-arthropod decomposers.

Global forest change and insect responses

Across the globe, forests are experiencing change (Hansen *et al*. 2013). Globally, mean annual temperatures have been increasing since the 1970's (Allen *et al*. 2010), with some work even suggesting an expansion of the earth's tropical belt (Seidel *et al*. 2008; Lu *et al*. 2009). Since 1900, the global average temperature has increased by 0.8 °C (Hansen *et al*. 2006), and since 1880 the 12 warmest years were all recorded between 1990 and 2005 (Lindner *et al*. 2010). Even conservative estimates of global climate change suggest increases in mean annual temperatures, significant drying in certain regions, and increases in the intensity and incidence of droughts (Christensen *et al*. 2007; Seager *et al*. 2007). The effect/s of such changes on forest functioning is not yet resolved. Possibly, certain forests might experience positive feedbacks, such as increased forest vigour and growth, higher water use efficiency, and extended growing seasons, whereas other forests might show negative responses (for example reduced growth, increases in stress, higher tree mortality rates, or disruption of plant-insect dynamics) (Ayres & Lombardero 2000; Bachelet *et al*. 2003; Lucht *et al*. 2006; Scholze *et al*. 2006; Lloyd & Bunn 2007; Allen *et al*. 2010). Due to the longevity of trees, forests are especially vulnerable to rapid changes in climate (Lindner *et al*. 2010).

Faunal biota associated with forest ecosystems are equally susceptible, with climate change already influencing species distributions and occurrence in forests. In the highland forests at Monte Verde in Costa Rica, for example, the golden toad (*Bufo periglenes*) has vanished, along with significant decreases in 42 of 113 species of the toad genus *Atelopus*. These observations are linked to warmer sea surface and air temperatures (Pounds & Crump1994; Pounds *et al*. 1997; Pounds *et al*. 1999; La Marca *et al*. 2005; Pounds *et al*. 2006). Apart from amphibians, evidence of insects (which are known to be sensitive to abiotic conditions (Gerlach *et al*. 2013)) responding to long-term changes in climate is steadily accumulating (Bale *et al*. 2002). Natural ecological disturbance is on the increase, with for example, the incidence of fire in the forests of Canada, Russia and Alaska increasing (Gillet *et al*. 2004; Soja *et al*. 2007). Stemming from subsequent warmer climatic conditions, insect outbreaks become affected (Berg *et al*. 2006). The spruce beetle (*Dendroctonus rufipennis*), for example (its numbers usually kept intact by cold and wet conditions), has caused large scale tree mortality, totalling approximately 1 million hectares of forest in Alaska following years of record warm temperatures (National Assessment Synthesis Team 2001). Forest insect range expansions are also occurring. The winter pine processionary moth (*Thaumetopoea pityocampa)* has shifted its elevation range following a record warm summer in southern Europe (Battisti et al. 2006). Its expanse in range to higher elevations were, during one summer, nearly a third of its total expansion during the previous three decades. This phenomenon is possibly linked to increased flight activity of newly emerged females with increases in temperature (Battisti et al. 2006). Expansions such as these could occur sporadically, with subsequent colder years causing range retractions not leading to long-term population settlement (Whittaker & Tribe 1998). Since the 1960’s, gradual north-eastern shifts in occurrence of *Operophtera brumata* (a temperature limited cyclic geometric moth) from the forests of Fennoscandia, Scandinavia, are linked to gradual increases in temperature, and not to spontaneous outbreaks outside its normal range (Jepsen *et al*. 2008). Evidently, range expansions of insects do not only occur relative to elevation, but also in latitude, and occur gradually over time. Forests in climates historically viewed as harsh for several insect herbivores might become increasingly exposed to establishment of new populations. The Boreal zone is a good example, lying beyond various insect’s distribution range (Lindner et al. 2010). However, increasing temperatures are expected to facilitate the northward expansion of two moth species, *Lymantria dispar* and *L. monacha* (Vanhanen et al. 2007), as well as that of *Neodiprion sertifer* (Virtanen et al. 1996; Veteli et al. 2005), a sawfly species, the larvae of which feeds on pine needles (Larsson & Tenow 1984). Evidently, insects associated with forests are greatly affected by changes in climate which severely affect their distributions and persistence in particular areas. As insects play disproportionately large roles in normal forest functioning, it means that understanding changes in insect distribution and behaviour is of critical importance for ecologists.

Climate change will not only affect insect populations directly, but also indirectly, by impacting on tree physiology. Nitrogen (N) supplies to plants can affect the productivity of herbivores by affecting both the quantity and nutritional quality of plants (Augustine *et al*. 2003; Craine *et al*. 2010). Foliar nitrogen, for example, increases during times of plant stress (Huberty & Denno 2004). Earlier work suggests that plant stress facilitates insect herbivore outbreak (White 1969; Mattson & Haack 1987). The plant-stress hypothesis (PSH) developed by White (1969) ascribes such outbreaks to changes in plant physiology during stressful times, specifically higher available levels of nitrogen. Generally, nitrogen is limiting for herbivorous insects (McNeill & Southwood 1978; Mattson 1980), with increases in available plant nitrogen attributed to outbreaks of herbivorous insects during stressful times (White 1969; 1974; 1984; 1993). However, there is still large discrepancy regarding the PSH with some authors, suggesting a decrease in insect herbivore performance during plant stress (Wearing & van Emden 1967; Wagner & Frantz 1990), with some work rejecting the PSH (for a review see Huberty & Denno 2004). Furthermore, reductions in turgor and water content during prolonged times of plant stress might adversely affect herbivore performance (Inbar *et al*. 2001; Huberty & Denno 2004).

Importantly, several studies point out a correlation between ^{15}N amount (rare stable isotope of nitrogen in plant tissues and soil) and precipitation, whether it be along an environmental gradient or defined geographical areas (Shearer *et al*. 1978; Heaton 1987; Fry 1991; Fogel & Johnson 1996; Austin & Vitousek 1998). Heaton (1987), for example, found a correlation between aridity and the ratio of $^{15}N/^{14}N$, with plants in wet sites (Knysna) having a lower foliar ^{15}N component than drier sites (Namib Desert). Handley *et al*. (1999) found a large effect of rainfall on foliar ^{15}N, ascribing it to the interaction of growth stimulating effects associated with increased rainfall. They further argue that any factor decreasing the proportional flux of ecosystem nitrogen (N) into organic matter storage pools conversely pushes ecosystem N toward ^{15}N-enrichment (Handley *et al*. 1999). These factors can refer to anything from aridity, salinity, extreme pH, fire or grazing. Another study further confirms this pattern, with an increase in foliar ^{15}N at drier sites compared to wetter sites in Hawaiian forests (Austin & Vitousek 1998). Temperature, too, has been found to influence the ratio of nitrogen stable isotopes, with higher mean annual temperatures resulting in a higher foliar ^{15}N/^{14}N ratio (Amundson *et al*. 2003). From the global patterns in linkages between N availability and ^{15}N, we can interpret the relationship between climate and foliar ^{15}N as drier, warmer ecosystems having higher N availability (Craine *et al*. 2009; Craine *et al*. 2015).

Whereas N availability generally increases in drier conditions, predictably affecting insect herbivores, carbon isotope discrimination also provides insight into environmental impacts on plant functioning (Diefendorf *et al*. 2010). For example, numerous studies have shown a decrease in ^{13}C (rare stable isotope of carbon) with increases in precipitation (Kohn 2010) and an increase in ^{13}C with increasing temperature (Wang *et al*. 2013). Warren *et al*. (2001) tested the hypothesis that levels of ^{13}C is a useful indication of water availability, and concluded it to be a useful indicator of drought stress / water availability. They found plant water potential to be highest during spring (after winter rains) and the lowest during late summer / autumn (before arrival of rain). Evidently, plants experiencing stress significantly affect insect herbivore phenology. With antagonistic (re: plant-herbivorous insect) interactions often highly specialized (Thebault & Fontaine 2010), long periods of stress could markedly impact such interactions.

Research aim and objectives

The Western Cape is predicted to be affected by global climate change in several ways, some of which include more hot days, higher average annual temperatures, and reduced average rainfall, especially in the western parts (Midgley *et al*. 2005). On a global scale, declines in forests are predicted to increase due to water limitation (Williams *et al*. 2013), with tree growth strongly dependent on water as well as nitrogen availability (Ibrahim *et al*. 1997). The largest forest complex in South Africa is situated in the southern Cape and, especially so for arthropod diversity, is still largely understudied. Botanically, the southern Cape forest complex has been extensively researched, with the focus mainly on tree production (e.g. Geldenhuys 1993a; Geldenhuys 1993b; Geldenhuys 1996; Vermeulen *et al*. 2012) and forest distribution (e.g. Geldenhuys 1991; Geldenhuys 1994). Some other research in South Africa's largest forest complex includes work on birds (Koen 1988) and limited work on invertebrates (Koen & Crowe 1987). Recent work investigated both edge and road effects on local forest arthropod diversity (Swart et al. 2018; Swart et al. 2019). However, holistic research on arthropods in the southern Cape forest complex and forests to the west of the southern Cape complex is absent, with arthropod research being done mostly in the fynbos (e.g. Wright 1993; Wright & Samways 1998; Giliomee 2003; Augustyn et al. 2013; Vrdoljak & Samways 2014; Lee & Barnard 2015) and succulent Karoo biomes (e.g. Wright & Samways 1996; Braschler *et al*. 2012). Importantly, no study to date has aimed to assess the interaction between indigenous forest trees in this region with associated arthropods, nor has any study predicted how future environmental change might alter such interactions.

The main aim of this thesis is to discern the relative effects of various aspects regarding landscape level effects, plot level effects, species level effects, and physiological level effects of forest trees on the arthropod diversity associated with trees. This is divided into four objectives, collectively comprising the four data chapters of this study.

Chapter 2*

*This chapter has been accepted for publication in *Ecological Entomology*, and is included here in its published form:

Swart, R. C., Samways, M. J., Pryke, J. S., & Roets, F. (2019). Individual tree context and contrast dictate tree physiological features and arthropod biodiversity patterns across multiple trophic levels. *Ecological Entomology (in press)*.

The first objective is to evaluate how tree-level context and contrast might dictate canopy arthropods associated with a tree. The respective effects of context and contrast has been discussed at the landscape-level (Wiens *et al*. 1993; Tscharntke *et al*. 2002). However, due to the relatively high diversity of fauna contained in tree canopies, these same factors might be equally applicable at a much finer scale, the individual tree. For this objective, I selected a single indigenous tree species, *Podocarpus elongatus*, occurring both as a forest tree in sheltered mountain kloof forests, and as a very large shrub on rock screes, in its natural environment. This species is also widely planted in suburban and urban environments in towns surrounding its natural habitat, the south Western Cape. I selected trees based on predetermined criteria, regarding its context (natural, semi-natural, planted) and its contrast to surrounding vegetation (high, low). Canopies of focal trees were fogged with chemical pyrethroids, in order to sample arthropods from the foliage and branches. The diversity patterns of arthropods collected were then compared between the various tree categories to determine the effects of where a tree is growing in the landscape on its ability to host canopy arthropods. Resultantly, I answer the first objective of whether the immediate surroundings of an individual tree might affect its associated biota, and to what extent.

Chapter 3*

*This chapter has been submitted for publication in a scientific journal (*Applied Soil Ecology*), and is included here in its submitted form.

The second objective is to determine the role of various tree species on detritivorous arthropod diversity patterns and leaf litter decomposition, and asking whether or not home-field advantage exists within single forests between different forest tree species. This was done in an indigenous southern Afrotemperate forest at the western extremity of these forests' range, Oubos (descriptions of study forests at the end of this chapter). I selected three dominant forest tree species, *Olea capensis macrocarpa*, *Podocarpus latifolius* and *Rapanea melanophloeos*, and firstly wanted to determine whether the detritivorous arthropods in forest leaf litter respond towards identity of a source tree's leaves. Secondly, I determine whether trees in diverse, mixed forests, create heterogeneous patches of arthropod diversity on the forest floor due to leaf-fall and build-up beneath source trees, and how this might impact leaf litter decomposition. Effectively, I answer the question of whether or not home-field advantage might occur at the tree-level in an indigenous forest. Also, I ascertain whether species of tree affect not only the arthropod diversity in canopies, as has been shown in numerous global studies, but also the arthropods associated with the breakdown of its leaves on forest floors.

Chapter 4

Here, I aim to answer unresolved questions with regards to forest functioning in a changing environment by focussing on five southern Afrotemperate forests along a large biogeographical gradient (>390 km) in the Western and Eastern Cape of South Africa (details of each of the five forests are given at the end of this chapter). Specifically, the third objective is to evaluate, for the first time, the canopy arthropod diversity of southern Afrotemperate forests, and how it responds to not only tree species identity and plot characteristics, but also to tree physiological features. This I then linked with predictions of future global change, focussing on rising levels of CO^2, increases in ambient temperatures, higher occurrences and incidences of drought, and increases in pollution. For this objective, I sampled canopy arthropods from 120 individual trees from 8 tree species, in the largest forest complex in South Africa, by means of chemical fogging.

Chapter 5

The fourth objective is to describe, and place in a global context, the canopy arthropod diversity associated with indigenous southern Afrotemperate forest trees. Africa represents one of the largest geographical gaps in canopy science, and especially the forests forming part of the Afromontane archipelago, has received close to zero attention with regards to not only its canopy arthropod diversity, but its entire forest arthropod diversity. I review the global literature, and discuss the patterns in diversity, of the major arthropod taxonomic groups sampled.

A short description of each forest included in this study (with the exception of the first data chapter) is detailed below.

Oubos. Oubos forest lies near the town of Riviersonderend, at the foothills of the Riviersonderend Mountains. The forest comprises of a large main patch with many smaller strips of forest linked to the larger patch, totalling around 381 ha in size. It is the most westerly forest and also the most species poor in terms of floral diversity. Although it is situated in a strictly winter rainfall area, the forest itself receives rainfall throughout the year due to orographic precipitation (± 1000 mm annually), creating a rain shadow effect on the northern side of the mountain (Le Maitre 2009). Dominant emergent species include *Olea capensis subs. macrocarpa*, *Rapanea melanophloeos*, *Olinia ventosa*, *Platylophus trifoliatus* and *Curtisia dentata*. The understorey is generally sparse and dominated by *Canthium inerme, Maytenus acuminata, Diospyros whyteana, Halleria lucida* and *Cassinopsis ilicifolia.* The closest large forest patch to Oubos is the Koloniesbos-Duiwelsbos complex near Swellendam, is 56.96 km away to the east. Between Oubos and the next study forest, Grootvadersbosch, lies 92.71 km. These two forests are further separated by the wide Breede River Valley which splits the Riviersonderend Mountains to the west from the Langeberg Mountains to the east.

Grootvadersbosch. Grootvadersbosch lies northwest of the town of Heidelberg at the foothills of the Langeberg Mountain Range. It is close in size to Oubos, at about 357 ha. Although situated in a winter rainfall area, this forest receives rain throughout the year similarly to Oubos. To the north east of Grootvadersbosch lies another relatively large indigenous forest, Boosmansbos, approximately 8.90 km away. Emergent tree species that occur here and not in Oubos include *Afrocarpus falcatus, Elaeodendron croceum* and *Ekebergia capensis*. The dominant overstorey species are similar to those found in Oubos, but with *Podocarpus latifolius*, *Ocotea bullata*, *Scolopia zeyheri* and *Cassine peragua* being more common. The understorey species are mostly similar to those found in Oubos, with *Burchelia bubalina* being the exception by being absent in Oubos. Along the same mountain range lies the next forest site, Kleinbos, 122.22 km to the east. With the exception of very few and very small forest patches, the area between Grootvadersbosch and Kleinbos is mostly dominated by mountain fynbos and farmland.

Kleinbos. This forest is the smallest of the five patches at only 200 ha. However, due to its more easterly location it contains species not found in Grootvadersbosch, including *Gonioma kamassi* and *Trichocladus crinitus*, both species that make up the majority of the understorey biomass. *Pterocelastrus tricuspidatus* becomes especially more abundant in Kleinbos (and the forests to the east) compared to the more westerly forests. Kleinbos receives rainfall throughout the year due to orographic precipitation and lies in the transition zone between winter- and all year rainfall. The overstorey species are similar to those found in Grootvadersbosch, but with the species *Nuxia floribunda* being a common overstorey component not found in Grootvadersbosch. The closest large forest patch to Kleinbos is in the mountains north of George, southern Cape, approximately 30.75 km to the east. From here, the largest continuous forest in South Africa starts its distribution, moving east to Humansdorp.

Woodville. Woodville forest forms part of the large, continuous southern Cape forest complex. On its own, it is about 504 ha, and lies 44.44 km east of Kleinbos. It lies in an all year rainfall region. It shares almost all its woody species with Kleinbos, but with some species only occurring in Woodville and further eastwards, including *Maytenus peduncularis*, *Ochna arborea*, *Trimeria grandifolia* and *Dovyalis rhamnoides*. In terms of understorey, there is little difference between Kleinbos and Woodville, with the dominant understorey trees being *Trichocladus crinitus*, *Gonioma kamassi* and various tree saplings. To the west of Woodville lies the relatively large Saasveld indigenous forest (± 450 m away) and to the east, across the Woodville River, lies the Bergplaas forest (± 200 m away), creating a large, continuous forest. Whereas Woodville is in close proximity to the nearby intact forests, Oubos, Grootvadersbosch and Kleinbos are relatively isolated in the landscape.

Witelsbos. Between Woodville and Witelsbos, the next study forest, lies 137.4 km of interspersed forests, fynbos, farms and settlements. This stretch occupies the largest forest complex in South Africa. Witelsbos is 379 ha, occurring east of the Storms River in the Eastern Cape Province. It forms part of a network of large indigenous patches that are isolated by farmlands or plantations, with the nearest large forest to Witelsbos being only 1.49 km to the southwest. Forming part of a single complex, species found in Witelsbos are nearly identical to those found in Woodville, and to a lesser extent in Kleinbos. However, *Brachylaena glabra* only starts its easterly distribution in Witelsbos and forms, together with

Trichocladus crinitus the bulk of the understorey plant biomass. The overstorey species are mostly identical to those found in Woodville.

Chapter 6

The final chapter is a general discussion and conclusion of this thesis.

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Chapter 2

Individual tree context and contrast dictate tree physiological features and arthropod biodiversity patterns across multiple trophic levels

Abstract

We tested the hypothesis that tree context (natural, semi-natural, or planted) and contrast (height of surrounding vegetation) affects tree physiological characters (leaf size, nutrient content, and stress-related factors), and also alter the arthropod biodiversity patterns either directly or indirectly. Arthropods were collected from tree canopies using chemical fogging from the ecologically important South African native tree *Podocarpus elongatus*. Low contrast trees had significantly larger leaves than those in high contrast environments and harboured overall higher richness, abundance and biomass of arthropods, but this was guild dependent. Trees in natural contexts had less foliar δ13C, suffered less from artificial nitrogen enrichment and harboured significantly higher herbivore and predator arthropod richness and unique assemblages compared to planted trees. Semi-natural trees supported natural levels of arthropod richness, but these were mostly generalist species. Tree context and contrast can therefore dictate associated biota at multiple trophic levels and native trees may fail to maintain natural biodiversity in transformed landscapes.

Keywords: Insect conservation, landscape ecology, tree-insect interactions, trophic cascades, urban conservation

Introduction

There are an estimated 61 000 species of trees globally (Qian *et al*. 2018), worth conserving in their own right. However, the total biodiversity solely dependent on trees is huge (i.e. Erwin 1982; Belsky 1994). For example, there are about 3 million species of arthropods restricted to tropical forests alone (Hamilton *et al*. 2010), many of which are restricted to tree canopies (Ozanne *et al*. 2003). Most of this diversity is yet to be described, and the forest canopy has therefore appropriately been dubbed ‘the last biotic frontier' (Erwin 1983; Bouget *et al*. 2011). The ability of trees to act as hosts for associated biodiversity in both natural (Allison *et al*. 1997) and transformed (Le Roux *et al*. 2018) landscapes is due to several factors. Trees create unique, elevated microhabitats that are very different from those of lower-growing vegetation (Manning *et al*. 2006). They also show strong inter- and intraspecific differences in factors such as tree height, leaf size, canopy density, chemical defences, and nutrient levels that might drive diversification of tree-associated arthropods (Wardhaugh *et al*. 2013). However, due to methodological constraints, very few studies have evaluated the response of arthropod assemblages to changes in biotic and abiotic factors at tree canopy height (Nakamura *et al*. 2017).

Immediate surroundings of individual trees may influence associated biota. Using tenets of landscape ecology (Wiens *et al*. 1993; Tscharntke *et al*. 2002), differences in where individual trees grow can create different microhabitats, each supporting uniquely adapted biodiversity. For example, trees that grow as scattered individuals in an open landscape (i.e. high contrast) are possibly affected differently by abiotic stressors (i.e. wind exposure, light availability, and/or soil moisture) relative to trees that grow in thickets or forests (i.e. low contrast) (Manning *et al*. 2006), which may have cascading effects on their associated arthropods. This occurs at forest community level, where high-contrast forest edges have different microclimates and arthropod assemblages compared to low-contrast forest edges (Pohlman *et al*. 2007; Swart *et al*. 2018). In addition, the context in which a forest patch occurs (i.e. whether the surrounding vegetation is natural or not) has a significant impact on the diversity of associated bees (Steffan-Dewenter *et al*. 2002), butterflies (Ricketts 2001), and even entire arthropod assemblages (Yekwayo *et al*. 2016). Although only tested at forest patch scale, we hypothesize that differences in context (natural or altered surroundings) and contrast (height differences with surrounding vegetation) will have substantial impacts on biota at a much finer scale, the individual tree (Le Roux *et al*. 2018).

The comparative importance of differences in context and contrast on individual tree-associated biota is currently unknown. Trees growing in isolation or in non-natural conditions may experience greater water stress than trees in a forest or in more natural conditions due to higher evapotranspiration rates (Giambelluca *et al*. 2009). Such water-stressed trees may become more prone (or even less prone) to attack by herbivorous arthropods, which, in turn, may affect other trophic levels (Hubberty & Denno 2004). Similarly, differences in context and contrast may affect the rate of photosynthesis, and therefore plant nutrient levels (e.g. total carbon and/or nitrogen content) that can have substantial effects on herbivores and subsequently other trophic levels (Meunier *et al*. 2016). In terms of context, native trees planted in urban environments may be exposed to greatly altered moisture and nutritive regimes, which have yet untested effects on associated biota. When the contrast between these individual trees and their surrounds are high, effects on associated biota may be even more severe. It has also been suggested that the phylogenetic similarity of the trees in close proximity to an individual tree has an effect on phytophagy (Yguel *et al*. 2011). Trees growing in altered contexts might experience severe changes in its phylogenetic similarity to trees growing in close proximity to it, compounding the effects on arthropod assemblages (Vialatte *et al.* 2010). Understanding these effects are important, as planting of native trees are promoted in urban environments to reduce impact on local tree-associated biodiversity (Alvey 2006), but their effectiveness in supporting high levels of biodiversity may be strongly hampered by surrounding factors (Sandström *et al*. 2006).

To the best of our knowledge, the combination of the tenets of habitat context and contrast, often used in landscape ecology, has not been evaluated at the individual tree level for a single native species. Landscape context alone has recently been investigated as a driver of differences in assemblages of birds, bats, and tree-trunk associated arthropods on various *Eucalyptus* tree species in south-eastern Australia (Le Roux *et al*. 2018). The authors found that differences in landscape context had little effect on the diversity of arthropods (abundance and species richness) on the tree trunk, with the exception of spiders and flies, with significant differences in assemblage composition of various arthropod groups (Le Roux *et al*. 2018). However, the sampling methods used (one glue trap per tree combined with active searching) are likely not comparable to the arthropod assemblages at canopy level associated with the more palatable leaves (Adis *et al*. 1998). This is important, as the bulk of arthropod biodiversity associated with individual trees occurs within tree canopies (Nadkarni 1994).

We determine here the effects of landscape context and contrast on tree physiological characteristics and canopy-associated arthropods of multiple trophic levels for individual trees of a single species. We expect to observe differences in biota between trees within different contrasts and contexts and differences in factors, such as leaf size, water stress levels, and nutrient levels. Results of this study will lead to a greater understanding of the factors that drive responses of biotic communities to changes in small-scale landscape features, and to better contemporary conservation planning.

Materials and Methods

Study area, host tree and sampling design

The study was conducted in the Boland region of the South-western Cape, South Africa (Fig. 1). This area is characterized as a winter rainfall zone with a typical Mediterranean climate (Procheş *et al*. 2005). Two biomes spatially dominate this region: Fynbos, a highly diverse, fire adapted, shrub-like vegetation with few native trees and Afro-temperate forests, occurring in small, isolated patches in gorges (van Wilgen *et al*. 1990). The Breede River yellowwood tree, *Podocarpus elongatus* (Pinales: Podocarpaceae), was chosen as the focal tree species, as it is a common component of Afro-temperate forests, but also one of the few native forest trees that occurs in open areas and on rock screes, often growing as scattered individuals. It is also a common garden plant, widely cultivated for its hardiness and aesthetics. The focal tree, *P. elongatus*, is phylogenetically isolated in its natural context in our study area, as it is the only dominant, emergent gymnosperm in its natural habitat. Other South African podocarps do not overlap in distribution range with *P. elongatus* in our study area. However, members of this genus are often planted in towns and suburbs which could decrease its phylogenetic isolation in altered contexts. This South African endemic coniferous species is restricted to mountains in the winter rainfall region, and is easily recognised by its narrow, elongate, and spirally arranged leaves. As it is a wind-pollinated conifer, it does not provide sustenance for nectar and pollen feeding animals. It does however, produce fleshy receptacles on the fruit-like cones, dispersed by frugivorous birds and small mammals (Geldenhuys 1993).

We chose 18 tree individuals in and around the towns of Paarl, Somerset West, and Stellenbosch, based on predetermined criteria (Table 1; Fig. 1). Nine focal trees were selected in areas where the tree was present in a dense thicket surrounded by mature trees (low contrast settings), and nine other trees were selected in areas where the focal tree grew individually surrounded only by lower growing vegetation or rocks (high contrast settings). These focal trees (details of which are given below) were further subdivided based on their context, of which six were situated in a natural context, six in a semi-natural context, and six in a planted context (Table 1).

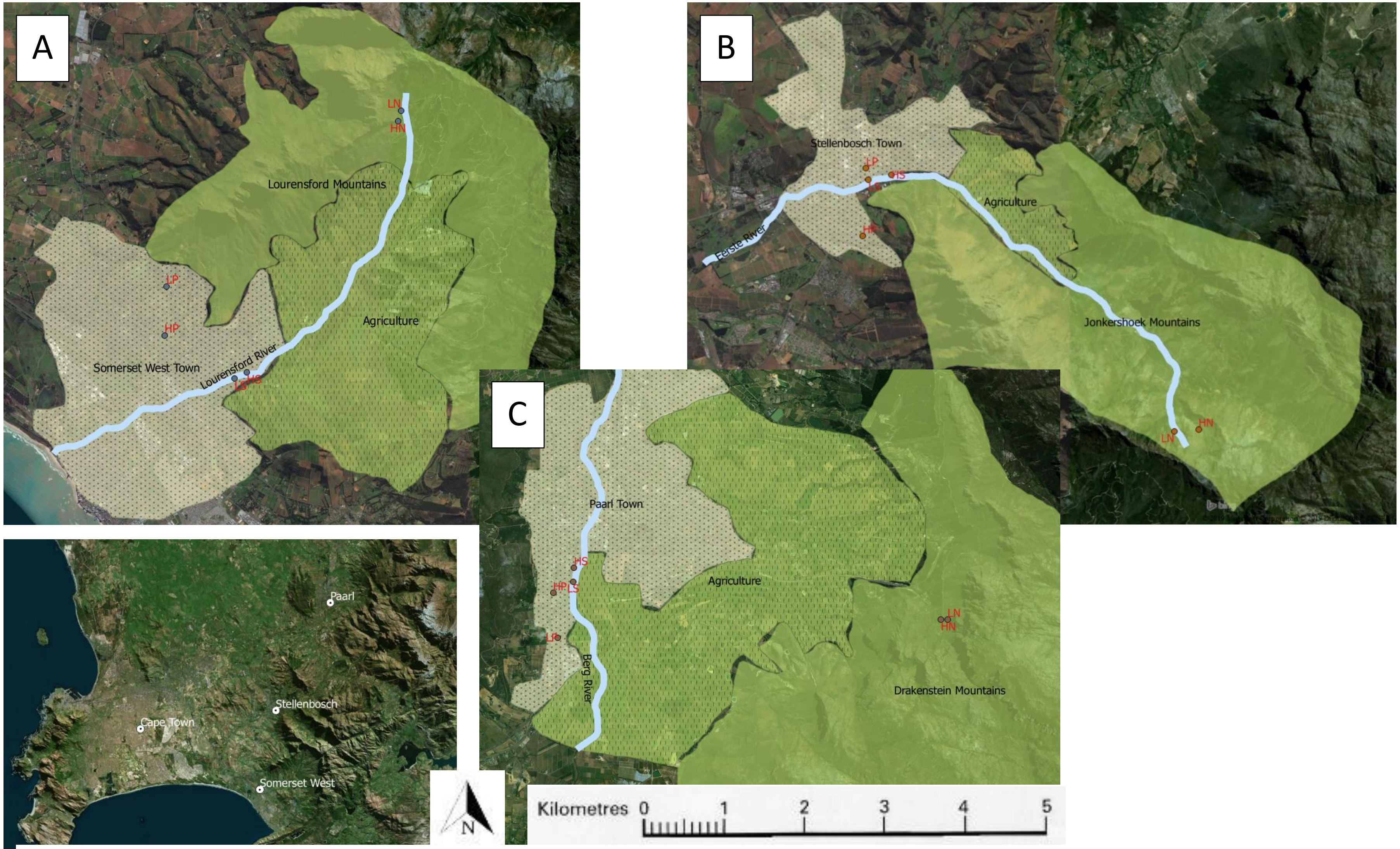

Figure 1: Study area in the Boland region, South Africa, illustrating the towns of Somerset West (A), Stellenbosch (B) and Paarl (C) as well as the locations of individual trees. Scale bar applicable to the three town maps. LN = Low Contrast, Natural Context; HN = High Contrast, Natural Context; LS = Low Contrast, Semi-natural Context; HS = High Contrast, Semi-natural Context; LP = Low Contrast, Planted Context; HP = High Contrast, Planted Context

Table 1: Criteria for selecting focal trees based on different contexts and contrasts.

Factor	**High Contrast (n = 9)**	**Low Contrast (n = 9)**
Natural (n = 6)	Growing individually in an undisturbed setting; surrounding trees at least 8 m away with canopies not touching the focal tree (n = 3).	Growing among other trees (different or same species) in an undisturbed forest setting, with canopies of surrounding trees touching the focal tree (n = 3).
Semi-Natural (n = 6)	Growing individually next to a river running through a suburban or urban setting; surrounding trees at least 8 m away with canopies not touching the focal tree. Trees most likely established through natural recruitment (n = 3).	Growing among other trees (different or same species) next to a river running through a suburban or urban setting, with canopies of surrounding trees touching the focal tree. Trees most likely established through natural recruitment (n = 3).
Planted (n = 6)	Growing individually in a transformed, suburban setting; surrounding trees at least 8 m away, with canopies not touching the focal tree. Trees were planted (n = 3).	Growing among other trees (different or same species) in a transformed, suburban setting, with canopies of surrounding trees touching the focal tree. Trees were planted (n = 3).

Plant characteristics

We standardized for tree selection as much as possible. The height of each tree was estimated by a single observer (mean height = 5.47 m ± 1.41; range 4 m – 8 m), with tree selecting standardized based on diameter at breast height, which had to be at least 60 cm. We randomly collected 200 leaves from each individual focal tree, and each leaf's length was measured. Leaf length was regarded as a good surrogate for leaf size in *P. elongatus*, as leaf length and leaf area of a particular plant species are often correlated (Nilsen & Webb 2007; Rivera et al. 2007). The leaves of *P. elongatus* are narrowly oblong, and typically drawn out in length, with leaf width rarely exceeding 5 mm compared to lengths of up to 60 mm (De Laubenfels 1985). Intact leaves (those with no visible damage) per tree were air dried for 4 months, milled and 0.02 g sent to the Stable Isotope Laboratory at the Department of Archaeology, University of Cape Town, South Africa to determine the total nitrogen and –carbon content, leaf

$\delta_{15}N/_{14}N$ and leaf $\delta_{13}C/_{12}C$. A study by Warren *et al*. (2001) demonstrated that levels of $\delta_{13}C$ are a useful indication of water availability, whereas nitrogen is a known limiting factor for herbivorous insects (Fagan *et al*. 2002). In addition, $\delta_{15}N/_{14}N$ values are often used to determine plant nitrogen sources (Handley & Raven 1992). In total, five physiological variables were measured for each tree: total nitrogen (%), $\delta_{15}N/_{14}N$, total carbon (%), $\delta_{13}C/_{12}C$ and leaf size.

Arthropod collection

Arthropods were sampled using machine fogging, as described by Adis *et al*. (1998), using a knock-down insecticide dispensed into the tree canopy as a column of fog, and then collecting falling arthropods at ground level. We used a Dyna-Fog IZ150TM fogging machine (fog particle size 0.5 – 50 micron; 42 litres per hour solution output) and a pyrethroid insecticide blend (1% deltamethrin, 0.6% permethrin, 6% piperonyl butoxide, 5% aromatic hydrocarbon solvent and 88% diesel) available as ready-mix from Dyna-Fog Africa. This insecticide was chosen for its rapid knockdown effect on arthropods, its rapid photo-degradation, and its low toxicity to vertebrates (Schleier & Peterson 2011). It also does not biomagnify in higher trophic levels (Schleier & Peterson 2011).

Before fogging, and only when needed, focal trees in the low contrast category were carefully cleared of small branches from neighbouring vegetation to ensure that arthropods sampled originated only from the focal tree. Two collecting sheets, each 320 cm x 148 cm in size and covering a combined area of 9.47 m^2, were placed directly under the canopy of the focal tree, ensuring that no branches of neighbouring trees were present directly above the sheets. Selected trees were treated with the insecticide (fogged) in the early morning hours (between 05:00 and 07:00) and only on windless days, to ensure that a maximum number of both nocturnal and diurnal taxa were present in samples. Sampling was conducted during the early summer months of November and December 2016, a peak time for local arthropod activity (Procheş & Cowling 2006). During this period, there is little rainfall, the sun rises early, and the female trees have not yet produced fleshy receptacles which might attract arthropod species not necessarily associated with only the leaves of the tree and might cause bias between male and female trees.

Fog was directed into the canopy of the focal tree for a total of 2 min, ensuring a constant volume of fog dispersed throughout the tree canopy. Collecting sheets were left under focal trees for 45 min after insecticide application to ensure maximal collection time, yet before larger arthropods recovered, after which time, all material on the collecting sheets were transferred to collecting jars and preserved in 70% ethanol.

Collected arthropods were sorted to morphospecies, and identified to order. Where possible, they were identified to family level, with spiders identified to genus and/or species level. Additionally, all arthropods were grouped according to their functional feeding guild based on examination of their mouthparts (Labandeira 1997) and the dominant feeding behaviour of the specific life stage of the specimen collected (Scholtz & Holm 1985). As the focal tree species is wind-pollinated, we excluded all pollen and nectar feeders from analyses, as these were likely tourists, which constituted a total of 31 individuals from 11 species. A reference collection of morphospecies are housed in the Entomology Museum, Stellenbosch University, with spiders housed at the South African National Collection of Arachnida, Pretoria.

Biomass of each morphospecies was calculated using models developed by Sample (1993) and Ganihar (1997) that derive biomass based on body dimensions (length and width) optimised per specific taxon. Length and width (at widest point on thorax or abdomen) of arthropods were measured using a digital calliper under a dissection microscope for increased accuracy. For each species, three randomly chosen individuals were measured, with the mean of each body dimension measurement calculated. All individuals of species that were represented only by 1 or 2 individuals were measured and averaged accordingly. An average biomass based on these measurements were then assigned per species. The model used for determining the biomass of spiders was the power model from Ganihar (1997), which uses only body length, and proven to fit spiders the best out of the four models they evaluated. Spider morphospecies that had average body lengths of less than 1.75 mm were excluded from biomass calculations due to model constraints (Ganihar 1997). All pseudoscorpions, ticks and mites were also excluded from biomass calculations due to their small size, and that no biomass model has been proposed for them to date. In total, 340 arthropods were excluded from a total of 5 409 individuals for all biomass calculations due to small size. Biomass of springtails and centipedes were calculated using the proposed models in Ganihar (1997). Biomass of all other taxa was calculated using the methodology proposed by Sample (1993).

Statistical analyses

For overall species estimates, as well as the respective arthropod groups, two non-parametric species estimators were used: the Chao2 and Jacknife2 estimators that reduce bias when dealing with small samples (Colwell & Coddington 1994), performed using PRIMER 6 (PRIMER-E 2008).

To test the effect of tree context and/or contrast on arthropod species richness, abundance and biomass, we constructed generalized linear mixed-effect models (GLMMs) in R (R Core Team 2013), using the package *lme4* (Bates *et al.* 2007). Factors included in the models were context, contrast, and the interaction between these two, with collection region (n = 6) included as a spatial random variable. Collecting region consisted of the three catchment areas of the mountain valleys in which sampling took place, subdivided into upper catchment and lower catchment areas. Poisson distributions with Laplace approximation were used to assess species richness (Bolker *et al*. 2009) and negative binomial distributions were implemented for both abundance and biomass data to correct for over-dispersion (Skaug *et al*. 2011). All plant characteristics (total leaf nitrogen (%), leaf δ15N/14N, total leaf carbon (%), leaf δ13C/12C and leaf size) means were found to be normally distributed, and linear modelling (LMERs), with context and contrast as fixed factors and collecting region again as spatial random variable, were constructed in R using the *lme4* package (Bates *et al*. 2007). Tukey post-hoc tests were performed on significant factors using the *multcomp* package in R (Hothorn *et al*. 2008).

To test the how plant characteristics (listed above) affected arthropod species richness, abundance, and biomass for each of the arthropod groups, various candidate models were evaluated. Relative support for the models were assessed using the AICc criterion with best model selection using the package *AICcmodavg* in R (Mazerolle 2019), after which Generalised Linear Mixed Models (GLMMs) were implemented using the candidate model with the lowest AICc. In the case where the lowest AICc value was obtained for the dummy model, it was assumed that none of the variables significantly explained the variation of the specific diversity measure for the guild tested. To visualise significant correlations, we created a scatterplot, plotting a trend line (with 95% confidence intervals) based on the GLMM of the relevant factor using the package *ggplot2* in R.

For assessing the compositional response of arthropod assemblages to the fixed factors (contrast and context), we constructed Bray-Curtis similarity matrices derived from square-root transformed abundance data to reduce the influence of common species (PRIMER-E 2008). Differences in arthropod assemblage composition between the respective contrasts and contexts, as well as the interaction between these factors, were evaluated using Permutational multivariate analyses of variance (PERMANOVA) in PRIMER 6 (PRIMER-E 2008), with collecting region included as a random variable.

To explain variation in species assemblage composition as described by the five measured plant characteristics, distance-based linear modelling (DistLM) was performed for each arthropod group, based on Bray-Curtis similarity matrices, using forward selection in PRIMER 6 (Clarke & Gorley 2006). This method allows for the addition of variables to the analyses based on their total variation explained until no further variables improve the model based on AICc (Burnham & Anderson 2004).

Results

Arthropod diversity

A total of 473 morphospecies were sampled from all *P. elongatus* trees, totalling 5 409 arthropod individuals. Herbivores accounted for 120 species, with a total of 55 chewers and 65 suckers. Predators contributed 103 morphospecies to overall species richness, and parasitoids 104. A total of 33 detritivore and 85 fly species were sampled, along with 14 ant species. Chao2 estimated an overall alpha diversity of 936 (± 77.8) and Jacknife2 estimated 917 species, indicating that sampling was not fully representative of the arthropod diversity associated with *P. elongatus*.

Effects of contrast and context on arthropod diversity

Species richness responded significantly to both contrast and context for overall arthropods (Table 2), with low contrast trees generally hosting more arthropod species than high contrast trees and planted trees hosting fewer species than semi-natural trees (Supplementary material, table S1). For overall herbivores, contrast had no effect. However, natural and semi-natural trees hosted higher species richness than planted trees. The chewers and suckers subgroups were significantly influenced by context only (Table 2; Supplementary material, table S1).

Low contrast trees had higher abundance for overall arthropods and parasitoids. Context affected only overall, parasitoid, and fly abundances, with semi-natural settings hosting significantly more flies compared to natural and planted trees, whereas overall and parasitoid abundances was greatest at semi-natural sites (Table 2; Supplementary material, table S1).

Contrast significantly affected the biomass of overall, herbivorous and chewing arthropods, with low contrast settings hosting a higher biomass of these groups (Tables 2; Supplementary material, table S1). Context only affected the biomass of flies (Table 2; Supplementary material, table S1).

Contrast had no effect on assemblage composition for any arthropod group. However, context significantly affected most groups (Table 2). For most groups, the natural context trees had unique assemblages compared to both semi-natural and planted contexts. Flies had similar assemblages between semi-natural and natural contexts.

Table 2: Comparisons of species richness, abundance and biomass of canopy-associated arthropods of *Podocarpus elongatus* tree individuals growing under different contrasts (high and low) and in different contexts (natural, semi-natural and planted), and the interaction as analysed using GLMMs [with Poisson distribution (species richness) or negative binomial distribution (abundance and biomass), and with collecting region as a random effect]. Estimates and standard errors are reported with degrees of freedom added in brackets after the factors. Pseudo-F values are presented for species compositional analyses generated by permutational multivariate analysis of variance (with collecting region as a random effect).

Species Richness	**Overall**	**Herbivores**	**Chewers**	**Suckers**	**Predators**	**Parasitoids**	**Detritivores**	**Flies**	**Ants**
	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE
Contrast (1)	**4.18 ± 0.18*** **	2.93 ± 0.18	2.14 ± 0.22	2.34 ± 0.22	2.99 ± 0.17	**2.04 ± 0.32** **	1.85 ± 0.22	**1.99 ± 0.21** **	1.19 ± 0.35
Context (2)	**3.95 ± 0.14*** **	**2.51 ± 0.19*** **	**1.38 ± 0.3** **	**2.09 ± 0.19** **	**2.77 ± 0.14*** **	**1.83 ± 0.26***	1.69 ± 0.18	**1.94 ± 0.18** **	1.04 ± 0.28
Contrast*Context (2)	**3.86 ± 0.2*** **	**2.63 ± 0.22** **	**1.63 ± 0.3** **	2.2 ± 0.26	**2.67 ± 0.21***	**1.67 ± 0.39*** **	1.71 ± 0.29	**1.37 ± 0.33** **	1.14 ± 0.41
Abundance									
	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE
Contrast (1)	**5.72 ± 0.36***	4.81 ± 0.38	3.57 ± 0.44	4.47 ± 0.4	4.69 ± 0.41	**3.08 ± 0.57***	3.3 ± 0.42	2.63 ± 0.39	3.2 ± 0.49
Context (2)	**5.36 ± 0.27***	3.89 ± 0.37	1.96 ± 0.03	3.73 ± 0.39	4.07 ± 0.31	**2.64 ± 0.46***	3.35 ± 0.33	**3.14 ± 0.49** **	3.49 ± 0.41
Contrast*Context (2)	**5.27 ± 0.35***	**4.43 ± 0.42***	**2.06 ± 0.49** **	**4.31 ± 0.47***	4.15 ± 0.46	**1.9 ± 0.57** **	2.91 ± 0.51	2.05 ± 0.45	3.58 ± 0.61
Biomass									
	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE
Contrast (1)	**6.38 ± 0.36***	**5.36 ± 0.4***	**4.7 ± 0.69** **	4.64 ± 0.39	**5.95 ± 0.35** **	1.18 ± 0.66	3.17 ± 0.53	1.98 ± 0.42	1.56 ± 0.64
Context (2)	5.81 ± 0.26	4.39 ± 0.35	2.02 ± 0.76	4.26 ± 0.36	**5.19 ± 0.38** **	1.89 ± 0.5	3.49 ± 0.44	2.53 ± 0.48	1.35 ± 0.47
Contrast*Context (2)	**5.75 ± 0.36***	4.54 ± 0.54	**1.88 ± 0.99***	4.75 ± 0.52	5.29 ± 0.38	**0.86 ± 0.66*** **	1.41 ± 0.71	1.42 ± 0.54	1.76 ± 0.69
Species Composition									
	Pseudo-F	Pseudo-F	Pseudo-F	Pseudo-F	Pseudo-F	Pseudo-F	Pseudo-F	Pseudo-F	Pseudo-F
Contrast (1)	0.97	0.75	0.49	0.95	0.78	1.33	0.64	1.12	0.86
Context (2)	**1.88*** **	**1.72***	1.41	**2.13***	**2.4*** **	1.03	1.49	**1.65***	1.8
Contrast*Context (2)	1.26	0.66	0.47	0.86	1.21	1.03	0.5	0.72	1.64

. P < 0.1, * P < 0.05, **P < 0.01, ***P < 0.001

Effects of contrast and context on plant characteristics

Five plant characteristics were measured: Leaf size, δ15N/14N, δ13C/12C, total nitrogen and total carbon (Table 3). Except for leaf size, being larger at low contrast settings (Table 3), none of the plant characteristics differed between the two contrasts. Tree context, however, affected all plant characteristics significantly, except total carbon and leaf size (Table 3). Natural settings were the only context where δ15N/14N was negative and differed significantly from both semi-natural and planted settings (Table 3). Natural settings also had the lowest δ13C/12C, significantly lower than semi-natural and planted settings (Table 3). Total nitrogen was highest at semi-natural contexts (Table 3).

Table 3: Results of the linear modelling reporting chi-square values for selected plant characteristics between the two contrast types and the three context types. Means reported under the Tukey post-hoc test are arranged from the highest mean to the lowest mean value.

Variable	**Contrast (1)**	**Context (2)**	**Tukey post hoc**
Leaf size	**6.10***	4.50	LC > HC
δ15N/14N	0.12	**13.78****	P ≥ SN > N
δ13C/12C	0.39	**14.19*****	SN ≥ P > N
Total nitrogen	0.74	**7.48***	SN ≥ N ≥ P; SN > P
Total carbon	2.16	0.16	-

LC = Low Contrast; HC = High Contrast; N = Natural context; SN = Semi-natural context; P = Planted context. Tukey post hoc arranged from highest mean to lowest mean; ≥ indicates the specific variable was higher but non-significant; > indicates the means differ significantly for the specific variable.

Degrees of freedom added in brackets after each factor.

* P < 0.05, **P < 0.01, ***P < 0.001.

Effects of plant characteristics on arthropod diversity

Overall arthropod species richness significantly correlated with three measured plant characteristics (Table 4). Leaf size, δ15N/14N and total nitrogen all positively correlated with overall species richness. The δ13C/12C negatively correlated with species richness of chewers (Fig. 2), detritivores and ants (Table 4). Total nitrogen also positively correlated with overall, sucker, predator, and fly species richness. The δ15N/14N correlated with overall, herbivore, parasitoid, and fly species richness (positively).

Table 4: Results of the best candidate models indicating relationships between plant characteristics and species richness, abundance, and biomass for each of the respective arthropod guilds sampled from *Podocarpus elongatus* trees. Reported model estimates and standard errors.

Guild	Variable	Species richness	Abundance	Biomass
Overall	Total N	**147.4 ± 26.5*** **	-	-
	δ15N/14N	**0.1 ± 0.02*** **	-	-
	Total C	-	-	-
	δ13C/12C	-	-	-
	Leaf size	**0.3 ± 0.1*** **	**0.4 ± 0.1** **	-
Herbivores	Total N	-	-	-
	δ15N/14N	**0.1 ± 0.05** **	-	-
	Total C	-	-	-
	δ13C/12C	-	**(-) 0.4 ± 0.1* **	-
	Leaf size	**0.5 ± 0.1*** **	-	-
Chewers	Total N	-	-	-
	δ15N/14N	-	-	-
	Total C	-	-	-
	δ13C/12C	**(-) 0.5 ± 0.1*** **	**(-) 0.9 ± 0.1*** **	**(-) 0.9 ± 0.3** **
	Leaf size	**0.5 ± 0.1*** **	**1 ± 0.2*** **	**1.9 ± 0.4*** **
Suckers	Total N	**121.9 ± 48.2* **	-	-
	δ15N/14N	-	-	-
	Total C	-	-	-
	δ13C/12C	-	-	-
	Leaf size	-	-	-
Predators	Total N	**272.7 ± 46.7*** **	**552.7 ± 62.8*** **	**640.4 ± 49*** **
	δ15N/14N	-	-	-
	Total C	-	**54.4 ± 18.1** **	**107.2 ± 26.8*** **
	δ13C/12C	(-) 0.19 ± 0.1.	**(-) 0.6 ± 0.2*** **	**(-) 0.8 ± 0.2*** **
	Leaf size	-	-	-
Parasitoids	Total N	-	-	-
	δ15N/14N	**0.3 ± 0.1*** **	-	**0.7 ± 0.1*** **
	Total C	-	-	**100.9 ± 1.1*** **
	δ13C/12C	-	-	-
	Leaf size	**0.7 ± 0.2*** **	-	**1.4 ± 0.2*** **
Detritivores	Total N	-	-	
	δ15N/14N	-	-	
	Total C	-	-	
	δ13C/12C	**(-) 0.2 ± 0.1** **	-	
	Leaf size	-	**0.9 ± 0.2*** **	**0.9 ± 0.3** **
Flies	Total N	**149.3 ± 66.1* **	-	-
	δ15N/14N	**0.1 ± 0.05* **	-	-
	Total C	-	-	-
	δ13C/12C	-	-	-
	Leaf size	**0.6 ± 0.2** **	-	-

Ants	Total N	-	**(-) 374.4 ± 82*****	-
	δ15N/14N	-	-	**(-) 440.5 ± 166.1****
	Total C	-	-	-
	δ13C/12C	**(-) 0.3 ± 0.1***	-	-
	Leaf size	-	-	-

. P < 0.1, * P < 0.05, **P < 0.01, ***P < 0.001

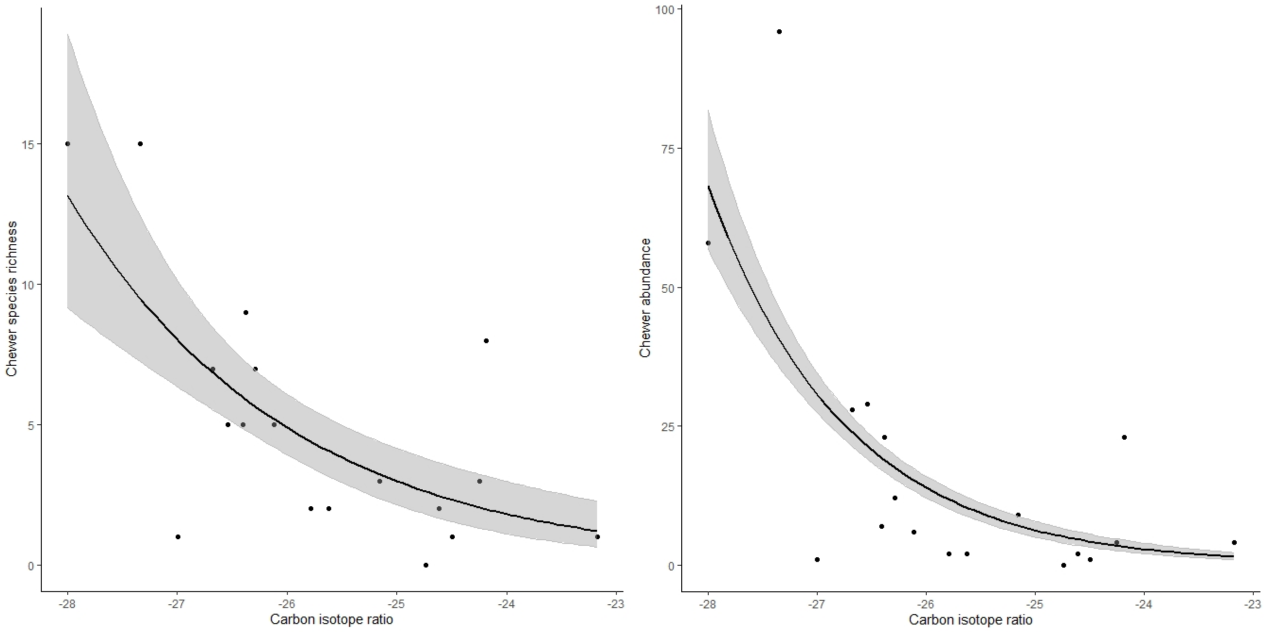

Figure 2: Scatterplot of chewer species richness (a) and abundance (b) in response to carbon isotope ratios for canopy-associated species from *Podocarpus elongatus* trees. The generalised linear response (with Poisson distribution and log-link function) is plotted as the black line and the 95% confidence level around this line as the shaded grey area.

The δ13C/12C significantly negatively correlated with herbivore, chewer (Fig. 2), and predator abundance. Overall, chewer and detritivore abundance positively correlated to leaf size. Interestingly, ant abundance negatively correlated with leaf total nitrogen content, and predator abundance positively (Table 4).

Chewer biomass correlated negatively to increases in the δ13C/12C, but positively to increase in leaf size. Predator biomass also negatively correlated with δ13C/12C, but positively with total foliar N and C. Detritivore biomass positively correlated with leaf size. Ant biomass had a negative correlation with δ15N/14N (Table 4).

Overall arthropod assemblages were unaffected by plant characteristics (Table 5). However, leaf size explained much of the variation in detritivore assemblage composition, with the δ13C/12C values explaining a significant amount of the variation in herbivore, chewer, and predator assemblage composition (Table 5). Total leaf nitrogen explained 18.47% of the variation in ant assemblage composition (Table 5).

Table 5: Results of the distance-based linear modelling (DistLM) sequential tests, indicating the most descriptive plant characteristics for each of the selected arthropod guilds' assemblage composition.

Guild	Variable	Pseudo-F	Variation explained (%)
Overall	-	-	-
Herbivores	δ13C/12C	**1.16****	11.88
Chewers	δ13C/12C	**2.70****	14.41
Suckers	δ15N/14N	**1.88***	10.5
Predators	δ13C/12C	**2.06****	11.41
Parasitoids	-	-	-
Detritivores	Leaf size	**3.4****	17.57
Flies	-	-	-
Ants	Total N	**3.63****	18.47

. P < 0.1, * P < 0.05, **P < 0.01, ***P < 0.001

Discussion

Trees are considered to support disproportionately high levels of associated biodiversity, and this was reaffirmed by our results. We collected nearly 500 arthropod species from a single tree species in a fairly restricted part of its entire geographical range, with estimates nearing 1 000. Additionally, we demonstrated that both contrast and context of the tree relative to its surrounds have notable effects on the tree-associated biota. For assemblage composition, trees in natural contexts hosted unique assemblages, indicating decreased canopy-associated arthropod diversity when tree context is altered. Also, trees in semi-natural and planted contexts hosted similar assemblages of most arthropod groups, indicating that these trees are likely unable to host the full range of naturally associated arthropod diversity, and possibly host comparatively higher numbers of generalist species (Didham *et al*. 1996).

Trees in high contrast environments had significantly smaller leaves than trees in low contrast environments. Traits of trees can vary according to different levels of light availability (Niinemets *et al*. 2015). Higher light availability, as expected in high contrast environments, could lead to decreases in leaf area (Keenan & Niinemets 2017). Possibly factors, such as light limitation in low contrast settings, could cause enhanced leaf surface area growth that, in turn, would increase the area for higher arthropod diversity, shown here for herbivore chewers. Leaf size is genetically determined, but can greatly vary based on herbivore pressure, light limitation, damage and/or drought (Peschiutta *et al*. 2018). Thus, interactions between a tree and its abiotic environment might directly affect associated primary consumers through altered tree physiology and/or morphology.

Tree contrast can also affect microclimatic conditions. For example, evidence suggests that wasps with narrow thermal ranges, or species adapted to cooler, shaded micro-climates associated with trees in forest interiors, struggle to adapt to higher temperatures associated with trees near forest edges, causing hymenopteran numbers to decrease (Deutsch *et al*. 2008; Stangler *et al*. 2015). Besides increased temperatures, trees in high contrast environments can also have reduced humidity levels (Chen *et al*. 1993), more wind exposure (Ewers & Didham 2007), and could be more susceptible to drought (Laurance *et al*. 2001), all of which that may also directly influence associated biota.

Total foliar N was highest in semi-natural settings, in trees next to rivers running through urban areas. This is likely ascribed to increased N availability in these rivers due to fertilizer inputs from farms upstream to these localities (Seitzinger *et al*. 2010; Liu *et al.* 2012). Whereas initially such increases in N might be beneficial to tree growth (Guerrieri *et al*. 2009), it may also boost the numbers of antagonistic organisms such as herbivores (Li *et al*. 2016). It is therefore not surprising that the increases in N in the present study, as in other studies, coincided with increases in species richness for overall and sucker arthropods (Letourneau *et al*. 1996; Schoonhoven *et al*. 2005). Moreover, the source of nitrogen in trees seemed to have little effect on tree-associated biota. Semi-natural and planted trees had positive δ15N/14N compared to natural trees, which had a negative ratio. This relates to the source of N (Takebayashi *et al*. 2010), where positive values of δ15N/14N are generally derived from pollutants such as vehicle emissions (Ammann *et al*. 1999, Saurer *et al*. 2004) (but see Choi *et al*. 2005; Bukata & Kyser 2007 for examples of the opposite). If the trees in the natural contexts here are assumed to have natural δ15N/14N, deviations reported here at semi-natural and planted contexts show clear disturbance from anthropogenic activities, be it agricultural or urban (Guerrieri *et al*. 2009).

Trees in natural contexts had lower δ_{13}C isotope values than trees in both semi-natural and planted contexts. The δ_{13}C isotope composition in plants often indicates water stress, especially in seasonally dry climates such as the southern part of the Western Cape (Warren *et al*. 2001; Walker *et al*. 2015). When plants experience water stress, CO_2 uptake is reduced, due to stomatal closure causing less discrimination against $^{13}CO_2$ and subsequently affects δ13C/12C (Walker *et al*. 2015). We found significant negative correlations between increased δ_{13}C and diversity of arthropod groups, including chewer abundance, species richness and biomass, as well as strong effects on most arthropod assemblage compositions.

A recent south-eastern Australia study revealed little effect of context on tree trunk arthropod abundance and species richness, except for spiders and flies, but significant effects on species compositions were evident (Le Roux *et al*. 2018). The authors found spider species richness to increase on trees in modified landscapes compared to reserves, whereas our study shows a significant drop in predator species richness in planted contexts compared to natural contexts. However, the semi-natural context is more representative of a modified landscape in their study, and had high predator species richness. Possibly, such intermediately disturbed areas greatly increase number of microhabitats (Devictor & Jiguet 2007) for generalist predaceous arthropods such as spiders (Oelbermann & Scheu 2002). Moreover, riparian areas generally provide spiders with a wider food range, even including aquatic insects that are not associated with trees themselves (Akamatsu *et al*. 2004). As seen here, and in Le Roux *et al*. (2018), the increased numbers of flies in semi-natural areas could further indirectly drive higher predator diversity in these landscapes.

With urban areas growing, conservation efforts are increasingly incorporating cityscapes (Goddard *et al*. 2010). As planted trees here supported less species than trees in semi-natural contexts, it is advisable that indigenous trees be planted in groups, or areas where they can propagate and establish small stands. Actions such as these, might mimic a tree's natural surroundings, and possibly reduce changes in its phylogenetic isolation, which could further impact its associated biota (Yguel *et al*. 2011). Otherwise biologically depauperate areas, such urban green spaces increase numbers of insects (Frederick & LeBuhn 2006), frogs (Carrier & Beebee 2003) and birds (Sandström *et al*. 2006). Comparing planted with semi-natural context trees, we suggest that such spaces be allowed to mimic natural succession, as spaces with a complex vegetation structure and a well-developed shrub layer can greatly increase biodiversity (Sandström *et al*. 2006). Also, urban ecological networks could help natural arthropod assemblages colonize indigenous trees outside natural areas through conservation corridors or stepping stone habitats (Ignatieva *et al*. 2010), but only when these networks are heterogeneous and representative of the natural flora (Pryke & Samways 2015).

Urban ecological networks will not only benefit the conservation of indigenous flora, but will also contribute to a more sustainable and resilient food web. For example, urban spaces with high levels of indigenous vegetation greatly increase reproduction successes of insectivorous birds dependent on higher arthropod abundances (Narango *et al*. 2018). When the reproductive successes of higher trophic levels are reduced due to collapses lower down, trophic cascades occur. This could greatly impact on ecosystem services in urban areas, including natural pest control by birds (Şekercioġlu *et al*. 2004) and carrion removal (Oaks *et al*. 2004). Our findings are therefore important for future urban landscape planning, suggesting here that native tree species needs to be propagated in urban green spaces, with ecological networks perhaps following rivers through towns, to better conserve tree-associated arthropod biota.

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Supplementary material

Table S1: Results of the Tukey post-hoc tests reporting z-values indicating differences in contrast and context of *Podocarpus elongatus* individuals for species richness, abundance, and biomass of the selected guilds with significance level indicated by stars. T-values are reported for PERMANOVA pairwise tests, indicating differences in species composition of the selected guilds. Only significant results (at the 5% probability level) are reported.

Species richness	**Contrast**	**Context**		
	Low vs. High	**Planted vs. Natural**	**Semi-Natural vs. Natural**	**Semi-Natural vs. Planted**
Overall	**4.4*****	(-) 2.1.	-	**8.5*****
Herbivores	-	**(-) 3.3****	-	**3.8*****
Chewers	-	**(-) 3.7*****	(-) 2.1.	2.2.
Suckers	-	(-) 2.1.	-	**3.1****
Predators	-	**(-) 2.5***	-	**4.7*****
Parasitoids	**2.9****	-	-	**2.8***
Detritivores	-	-	-	-
Flies	**2.6****	-	**2.4***	**4.9*****
Ants	-	-	-	-
Abundance	**Contrast**	**Context**		
	Low vs. High	**Planted vs. Natural**	**Semi-Natural vs. Natural**	**Semi-Natural vs. Planted**
Overall	**2.8****	-	-	**3.3****
Herbivores	-	-	-	-
Chewers	-	-	-	-
Suckers	-	-	-	-
Predators	-	-	-	-
Parasitoids	**2.6****	-	-	**2.8***
Detritivores	-	-	-	-
Flies	-	-	**2.8***	**4*****
Ants	-	-	-	-
Biomass	**Contrast**	**Context**		
	Low vs. High	**Planted vs. Natural**	**Semi-Natural vs. Natural**	**Semi-Natural vs. Planted**
Overall	**2.1***	-	-	-
Herbivores	**2.1***	-	-	-
Chewers	**3.1****	-	-	-
Suckers	-	-	-	-
Predators	-	-	-	-
Parasitoids	-	-	-	-
Detritivores	-	-	-	-
Flies	-	-	**2.6***	-
Ants	-	-	-	-
Species composition	**Contrast**	**Context**		
	Low vs. High	**Planted vs. Natural**	**Semi-Natural vs. Natural**	**Semi-Natural vs. Planted**
Overall	-	**1.3****	**1.4***	-
Herbivores	-	**1.4***	**1.3***	-
Chewers	-	-	-	-

Suckers	-	**1.5***	**1.5****	-
Predators	-	**1.6****	**1.6****	-
Parasitoids	-	-	-	-
Detritivores	-	-	-	-
Flies	-	-	-	**1.5****
Ants	-	-	-	-

. P < 0.1, * P < 0.05, **P < 0.01, ***P < 0.001

Table S2: Summary statistics for each variable compared between the different contrasts (n=9) and contexts (n=6).

	High Contrast				**Low Contrast**				**Natural**				**Semi-natural**				**Planted**			
Variable	**Mean**	SE	Min.	Max.	**Mean**	SE	Min.	Max.	**Mean**	SE	Min.	Max.	**Mean**	SE	Min.	Max.	**Mean**	SE	Min.	Max.
Leaf size	3.62	0.03	0.8	7.8	4.45	0.03	1	8.7	3.94	0.03	1	8.7	4.43	0.04	0.8	8.1	3.66	0.03	1.1	7.1
δ15N/14N	2.43	1.15	-2.54	6.87	2.17	0.61	-0.91	5.02	-0.28	0.54	-2.54	0.93	3.4	1.02	0.26	6.87	3.78	0.85	0.31	6.47
δ13C/12C	-25.61	0.32	-27	-24.19	-25.81	0.52	-28	-23.17	-26.72	0.34	-28	-25.79	-24.82	0.52	-26.42	-23.17	-25.59	0.41	-27	-24.5
Total nitrogen	0.011	0.002	0.008	0.02	0.012	0.002	0.009	0.02	0.012	0.001	0.01	0.01	0.013	0.001	0.01	0.02	0.011	0.001	0.01	0.01
Total carbon	0.47	0.006	0.46	0.48	0.47	0.007	0.46	0.48	0.47	0.003	0.46	0.48	0.47	0.003	0.46	0.48	0.47	0.002	0.46	0.48

SE = Standard error of the mean.

Table S3: Model selection results (based on Akaike Information Criterion for small sample sizes) for each arthropod group with its three respective diversity indices showing the first three candidate models through best model selection. K = number of parameters, ΔAICc = difference in AICc score between focal model and top-ranked model, AICc(weight) = model weight.

	Diversity indices											
	Species richness				**Abundance**				**Biomass**			
Guild	**Model**	**K**	**ΔAICc**	**AICc(weight)**	**Model**	**K**	**ΔAICc**	**AICc(weight)**	**Model**	**K**	**ΔAICc**	**AICc(weight)**
Overall	N + Niso + Size	5	0	0.74	Size	4	0	0.3	Intercept	3	0	0.24
	N + Niso + C + Size	6	2.88	0.17	Ciso + Size	5	1.83	0.12	Size	4	1	0.14
	N + Niso + Ciso + Size	6	4.57	0.08	intercept	3	2.39	0.09	Ciso	4	1.45	0.11
Herbivores	Niso + Size	4	0	0.23	Ciso	4	0	0.16	Intercept	3	0	0.25
	Size	3	0.71	0.16	intercept	3	0.29	0.14	Size	4	1.33	0.13
	N + Size	4	1.77	0.1	Size	4	0.36	0.13	Niso	4	1.41	0.13
Chewers	Ciso + Size	4	0	0.3	Ciso + Size	5	0	0.7	Ciso + Size	5	0	0.63
	N + C + Ciso	5	1.09	0.17	C + Ciso + Size	6	3.14	0.15	N + Ciso + Size	6	4.36	0.07
	N + C + Ciso + Size	6	1.44	0.15	N + Ciso + Size	6	4.07	0.09	C + Ciso + Size	6	4.47	0.07
Suckers	N	3	0	0.24	Intercept	3	0	0.22	Intercept	3	0	0.34
	Size	3	0.62	0.18	Ciso	4	1.07	0.13	C	4	1.22	0.18
	N + Size	4	1.62	0.11	Niso	4	1.45	0.11	Niso	4	3.06	0.07
Predators	N + Ciso	4	0	0.3	N + C + Ciso	6	0	0.42	N + C + Ciso	6	0	0.41
	N	3	0.15	0.27	N + Ciso	5	2.49	0.12	Intercept	3	1.88	0.16
	N + C + Ciso	5	2.24	0.1	N	4	2.77	0.1	Ciso	4	3.81	0.06
Parasitoids	Niso + Size	4	0	0.54	Intercept	3	0	0.16	C + Niso + Size	6	0	0.43
	N + Niso + Size	5	1.73	0.23	Size	4	0.21	0.14	N + Niso + C + Size	7	1.66	0.19
	C + Niso + Size	5	3.89	0.08	Ciso	4	0.47	0.12	Niso + Size	5	3.58	0.07
Detritivores	Ciso	3	0	0.27	Size	4	0	0.45	Size	4	0	0.47
	Intercept	2	1.02	0.16	C + Size	5	1.48	0.21	N + Size	5	3.25	0.09
	N + Ciso	4	2.45	0.08	N + Size	5	3.62	0.07	Niso + Size	5	3.31	0.09

Flies	N + Niso + Size	5	0	0.34	Intercept	3	0	0.16	Intercept	3	0	0.23
	N + Size	4	0.9	0.22	Size	4	0.23	0.14	Size	4	0.51	0.18
	Niso + Size	4	1.55	0.16	N + Size	5	0.85	0.1	Niso + Size	5	1.01	0.14
Ants	Ciso	3	0	0.18	N	4	0	0.41	N	4	0	0.35
	Intercept	2	0.2	0.16	N + Niso	5	1.84	0.16	N + Ciso	5	1.63	0.15
	Niso + Ciso	4	0.87	0.11	N + Size	5	3.15	0.08	N + C	5	3.31	0.07

Size = Leaf size; N = Total leaf nitrogen content; C = Total leaf carbon content; Niso = δ15N/14N; Ciso = δ13C/12C

Table S4: Species list of arthropods sampled from *Podocarpus elongatus* (n=18) by means of canopy fogging, with family and species name included where known, as well as feeding guild and type of herbivore where applicable.

Specimen number	Morpho Code	Order	Family	Species	Guild	Herbivore Type	Biomass (mg)	Abundance
1	Ara001a	Araneae	Trachelidae	*Afroceto martini*	Predator		3,636	19
2	Ara001b	Araneae	Gnaphosidae	*Poecilochroa anomala*	Predator		3,496	1
3	Ara002a	Araneae	Salticidae	*Dendryphantes purcelli*	Predator		5,889	11
4	Ara002b	Araneae	Salticidae	*Tusitala hirsuta*	Predator		5,676	2
5	Ara004	Araneae	Salticidae	*Dendryphantes silvestris*	Predator		1,333	11
6	Ara005	Araneae	Theridiidae	*Theridion sp. 1*	Predator		NA	1
7	Ara007	Araneae	Philodromidae	*Gephyrota glauca*	Predator		NA	5
8	Ara008a	Araneae	Theridiidae	*Theridion sp. 2*	Predator		2,501	4
9	Ara008b	Araneae	Theridiidae	*Theridion sp. 4*	Predator		2,501	5
10	Ara009	Araneae	Lycosidae	*Pardosa* sp.	Predator		1,375	2
11	Ara010	Araneae	Theridiidae	*Theridion sp. 3*	Predator		0,129	10
12	Ara011	Araneae	Theridiidae	*Phycosoma* sp. nov.	Predator		NA	1
13	Ara012	Araneae	Theridiidae	*Enoplognatha* sp.	Predator		NA	1
14	Ara013	Araneae	Gnaphosidae	*Zelotes* sp.	Predator		1,137	1
15	Ara014	Araneae	Araneidae	*Neoscona subfusca*	Predator		6,024	1
16	Ara018	Araneae	Thomisidae	*Oxytate* sp.	Predator		15,381	7
17	Ara019	Araneae	Oonopidae	*Opopaea mattica*	Predator		NA	5

18	Ara020	Araneae	Salticidae	*Thyene* sp.	Predator	NA	2
19	Ara021	Araneae	Araneidae	*Ursa* sp.	Predator	0,834	7
20	Ara022	Araneae	Salticidae	*Heliophanus* sp.	Predator	0,090	2
21	Ara024	Araneae	Theridiidae	*Theridion* sp. 5	Predator	NA	4
22	Ara026	Araneae	Clubionidae	*Clubiona* sp.	Predator	7,537	52
23	Ara028	Araneae	Salticidae	*Rumburak lateripunctatus*	Predator	2,098	4
24	Ara031	Araneae	Selenopidae	*Anyphops* sp.	Predator	1,289	3
25	Ara039	Araneae	Philodromidae	*Philodromus* sp.	Predator	NA	4
26	Ara041	Araneae	Araneidae	*Neoscona theisi theisiella*	Predator	148,984	1
27	Ara043	Araneae	Linyphiidae	*Agyneta* sp.	Predator	NA	4
28	Ara044	Araneae	Tetragnathidae	*Tetragnatha* sp.	Predator	2,732	2
29	Ara045	Araneae	Sparassidae	*Olios* sp.	Predator	3,556	8
30	Ara047	Araneae	Thomisidae	*Tmarus cameliformes*	Predator	0,518	3
31	Ara048	Araneae	Araneidae	*Neoscona* sp.	Predator	NA	1
32	Ara050	Araneae	Thomisidae	*Synema vallotoni*	Predator	0,554	1
33	Ara053	Araneae	Araneidae	*Larinia* sp. (possibly new)	Predator	5,466	3
34	Ara056	Araneae	Araneidae	*Neoscona blondeli*	Predator	5,102	1
35	Ara058	Araneae	Salticidae	*Thyene natali*	Predator	6,828	1
36	Ara059	Araneae	Thomisidae	*Pyrethesis* sp.	Predator	1,744	1
37	Blatt001	Blattodea	Blaberidae		Detritivore	13,453	3
38	Blatt002	Blattodea	Blattidae		Detritivore	24,391	3
39	Blatt003	Blattodea	Blattidae		Detritivore	1,270	3
40	Blatt004	Blattodea	Blattidae		Detritivore	4,984	1
41	Blatt005	Blattodea	Blaberidae		Detritivore	0,278	2
42	Blatt006	Blattodea	Blatellidae		Detritivore	1,083	13
43	Blatt007	Blattodea	Blattidae		Detritivore	1,462	1
44	Blatt008	Blattodea	Blaberidae		Detritivore	2,090	65
45	Ce001	Other (Diplopoda)			Detritivore	5,449	2
46	Ce002	Other (Diplopoda)			Detritivore	4,803	97
47	Col001	Coleoptera	Coccinellidae		Predator	9,346	138
48	Col002	Coleoptera	Carabidae		Predator	4,017	10

49	Col003	Coleoptera	Coccinellidae	Predator		0,832	56
50	Col004	Coleoptera	Scolytinae	Herbivore	Chewer	0,229	21
51	Col005	Coleoptera	Coccinellidae	Predator		1,249	48
52	Col006	Coleoptera	Cryptophagidae	Detritivore		0,186	34
53	Col007	Coleoptera	Coccinellidae	Predator		4,345	272
54	Col008	Coleoptera	Staphylinidae	Predator		0,063	35
55	Col009	Coleoptera	Anthicidae	Predator		0,466	9
56	Col010	Coleoptera	Cryptophagidae	Detritivore		0,088	8
57	Col011	Coleoptera	Elateridae	Herbivore	Chewer	2,512	1
58	Col012	Coleoptera	Phalacridae	Herbivore	Chewer	0,247	1
59	Col014	Coleoptera	Anthribidae	Herbivore	Chewer	0,305	26
60	Col015	Coleoptera	Scolytinae	Herbivore	Chewer	0,369	1
61	Col016	Coleoptera	Coccinellidae	Predator		1,395	1
62	Col017	Coleoptera	Ptilidae	Herbivore	Chewer	0,020	2
63	Col018	Coleoptera	Dermestidae	Detritivore		1,406	1
64	Col020	Coleoptera	Cleridae	Predator		0,757	2
65	Col021	Coleoptera	Scolytinae	Herbivore	Chewer	0,826	1
66	Col022	Coleoptera	Scraptiidae	Herbivore	Chewer	0,286	11
67	Col024	Coleoptera	Coccinellidae	Predator		17,140	5
68	Col025	Coleoptera	Curculionidae	Herbivore	Chewer	6,658	12
69	Col028	Coleoptera	Carabidae	Predator		0,962	1
70	Col029	Coleoptera	Tenebrionidae	Detritivore		33,559	2
71	Col030	Coleoptera	Scarabaeidae	Herbivore	Chewer	122,730	1
72	Col031	Coleoptera	Curculionidae	Herbivore	Chewer	0,226	2
73	Col032	Coleoptera	Pselaphidae	Predator		0,090	1
74	Col033	Coleoptera	Staphylinidae	Predator		0,096	6
75	Col034	Coleoptera	Chrysomelidae	Herbivore	Chewer	0,723	2
76	Col035	Coleoptera	Scolytinae	Herbivore	Chewer	0,166	5
77	Col036	Coleoptera	Curculionidae	Herbivore	Chewer	1,209	6
78	Col037	Coleoptera	Tenebrionidae	Detritivore		1,350	2
79	Col038	Coleoptera	Staphylinidae	Predator		0,032	1

80	Col040	Coleoptera	Phalacridae	Herbivore	Chewer	0,470	1
81	Col041	Coleoptera	Coccinellidae	Predator		0,898	2
82	Col042	Coleoptera	Elateridae	Herbivore	Chewer	4,661	3
83	Col043	Coleoptera	Carabidae	Predator		0,866	3
84	Col044	Coleoptera	Scolytinae	Herbivore	Chewer	0,560	1
85	Col045	Coleoptera	Anobiidae	Herbivore	Chewer	0,185	1
86	Col046	Coleoptera	Chrysomelidae	Herbivore	Chewer	0,228	4
87	Col047	Coleoptera	Curculionidae	Herbivore	Chewer	0,221	1
88	Col048	Coleoptera	Cleridae	Detritivore		0,218	4
89	Col049	Coleoptera	Chrysomelidae	Herbivore	Chewer	0,656	16
90	Col050	Coleoptera	Chrysomelidae	Herbivore	Chewer	2,007	20
91	Col051	Coleoptera	Clambidae	Fungivore		0,076	16
92	Col052	Coleoptera	Curculionidae	Herbivore	Chewer	0,058	21
93	Col054	Coleoptera	Curculionidae	Herbivore	Chewer	0,118	33
94	Col055	Coleoptera	Carabidae	Predator		31,651	4
95	Col056	Coleoptera	Cryptophagidae	Detritivore		0,515	1
96	Col058	Coleoptera	Coccinellidae	Predator		3,191	1
97	Col059	Coleoptera	Coccinellidae	Predator		0,128	17
98	Col061	Coleoptera	Coccinellidae	Predator		6,091	2
99	Col062	Coleoptera	Dermestidae	Detritivore		0,635	1
100	Col063	Coleoptera	Curculionidae	Herbivore	Chewer	0,608	1
101	Col064	Coleoptera	Chrysomelidae	Herbivore	Chewer	0,985	1
102	Col066	Coleoptera	Coccinellidae	Predator		9,244	1
103	Col067	Coleoptera	Coccinellidae	Predator		0,931	1
104	Col068	Coleoptera	Curculionidae	Herbivore	Chewer	0,754	1
105	Col069	Coleoptera	Carabidae	Predator		20,010	1
106	Col070	Coleoptera	Elateridae	Herbivore	Chewer	5,518	1
107	Col071	Coleoptera	Brentidae	Herbivore	Chewer	3,873	1
108	Col072	Coleoptera	Scolytinae	Herbivore	Chewer	0,050	1
109	Col074	Coleoptera	Anthicidae	Predator		0,344	1
110	Col075	Coleoptera	Curculionidae	Herbivore	Chewer	0,206	2

111	Col078	Coleoptera	Elateridae	Herbivore	Chewer	106,427	1
112	Col079	Coleoptera	Cantharidae	Predator		1,064	1
113	Col080	Coleoptera	Mordellidae	Herbivore	Chewer	0,568	1
114	Col081	Coleoptera	Curculionidae	Herbivore	Chewer	0,612	1
115	Col082	Coleoptera	Coccinellidae	Predator		6,481	1
116	Col083	Coleoptera	Melyridae	Predator		0,238	1
117	Col084	Coleoptera	Staphylinidae	Predator		0,564	1
118	Col085	Coleoptera	Anthribidae	Herbivore	Chewer	2,223	1
119	Col086	Coleoptera	Tenebrionidae	Detritivore		5,444	1
120	Col087	Coleoptera	Coccinellidae	Predator		0,419	1
121	Col088	Coleoptera	Coccinellidae	Predator		1,516	1
122	Col089	Coleoptera	Coccinellidae	Predator		1,945	1
123	Col090	Coleoptera	Curculionidae	Herbivore	Chewer	0,072	3
124	Col091	Coleoptera	Curculionidae	Herbivore	Chewer	0,451	1
125	Col092	Coleoptera	Nitidulidae	Detritivore		0,144	1
126	Col093	Coleoptera	Curculionidae	Herbivore	Chewer	0,074	43
127	Col094	Coleoptera	Scolytinae	Herbivore	Chewer	0,172	1
128	Col095	Coleoptera	Cleridae	Predator		0,503	1
129	Col096	Coleoptera	Cryptophagidae	Detritivore		0,165	3
130	Col097	Coleoptera	Staphylinidae	Predator		0,768	8
131	Col098	Coleoptera	Bruchidae	Herbivore	Chewer	0,589	12
132	Col099	Coleoptera	Cassidinae	Herbivore	Chewer	14,392	1
133	Col100	Coleoptera	Cassidinae	Herbivore	Chewer	23,568	1
134	Col101	Coleoptera	Staphylinidae	Predator		7,865	1
135	Col102	Coleoptera	Chrysomelidae	Herbivore	Chewer	0,718	4
136	Col104	Coleoptera	Bruchidae	Herbivore	Chewer	0,404	1
137	Dip001	Diptera		Diptera		0,573	3
138	Dip002	Diptera		Diptera		0,748	1
139	Dip003	Diptera		Diptera		0,346	2
140	Dip004	Diptera		Diptera		0,421	29
141	Dip005	Diptera		Diptera		0,090	81

142	Dip007	Diptera	Diptera	0,127	10
143	Dip008	Diptera	Diptera	0,124	21
144	Dip009	Diptera	Diptera	0,289	3
145	Dip010	Diptera	Diptera	1,024	9
146	Dip011	Diptera	Diptera	1,830	8
147	Dip012	Diptera	Diptera	0,120	32
148	Dip013	Diptera	Diptera	1,103	2
149	Dip014	Diptera	Diptera	1,188	11
150	Dip015	Diptera	Diptera	0,820	18
151	Dip016	Diptera	Diptera	0,076	51
152	Dip017	Diptera	Diptera	0,247	2
153	Dip018	Diptera	Diptera	1,716	32
154	Dip019	Diptera	Diptera	2,020	15
155	Dip020	Diptera	Diptera	0,129	7
156	Dip021	Diptera	Diptera	2,452	6
157	Dip023	Diptera	Diptera	0,096	1
158	Dip024	Diptera	Diptera	0,118	1
159	Dip025	Diptera	Diptera	0,106	9
160	Dip026	Diptera	Diptera	0,093	2
161	Dip027	Diptera	Diptera	0,045	3
162	Dip028	Diptera	Diptera	0,312	18
163	Dip029	Diptera	Diptera	0,549	3
164	Dip030	Diptera	Diptera	0,180	1
165	Dip031	Diptera	Diptera	0,082	1
166	Dip032	Diptera	Diptera	0,175	13
167	Dip033	Diptera	Diptera	0,288	1
168	Dip036	Diptera	Diptera	0,099	1
169	Dip037	Diptera	Diptera	0,088	1
170	Dip039	Diptera	Diptera	0,234	2
171	Dip041	Diptera	Diptera	0,239	6
172	Dip042	Diptera	Diptera	1,601	2

173	Dip043	Diptera	Diptera	2,780	5
174	Dip044	Diptera	Diptera	0,782	1
175	Dip045	Diptera	Diptera	0,734	2
176	Dip046	Diptera	Diptera	0,046	3
177	Dip047	Diptera	Diptera	0,023	1
178	Dip048	Diptera	Diptera	0,029	1
179	Dip049	Diptera	Diptera	0,270	1
180	Dip050	Diptera	Diptera	0,132	1
181	Dip053	Diptera	Diptera	0,892	1
182	Dip054	Diptera	Diptera	0,746	17
183	Dip055	Diptera	Diptera	0,374	1
184	Dip056	Diptera	Diptera	0,016	13
185	Dip057	Diptera	Diptera	0,120	1
186	Dip058	Diptera	Diptera	0,209	1
187	Dip059	Diptera	Diptera	0,871	3
188	Dip060	Diptera	Diptera	0,390	5
189	Dip061	Diptera	Diptera	1,508	1
190	Dip062	Diptera	Diptera	3,581	1
191	Dip063	Diptera	Diptera	7,634	1
192	Dip064	Diptera	Diptera	0,148	3
193	Dip065	Diptera	Diptera	0,049	2
194	Dip066	Diptera	Diptera	0,043	2
195	Dip067	Diptera	Diptera	0,038	2
196	Dip068	Diptera	Diptera	0,539	1
197	Dip069	Diptera	Diptera	0,045	2
198	Dip070	Diptera	Diptera	0,204	1
199	Dip071	Diptera	Diptera	0,126	1
200	Dip072	Diptera	Diptera	0,425	1
201	Dip074	Diptera	Diptera	0,051	1
202	Dip075	Diptera	Diptera	0,123	1
203	Dip076	Diptera	Diptera	0,425	1

204	Dip077	Diptera		Diptera		0,077	1
205	Dip078	Diptera		Diptera		0,611	10
206	Dip080	Diptera		Diptera		2,924	1
207	Dip081	Diptera		Diptera		1,572	1
208	Dip082	Diptera		Diptera		1,710	1
209	Dip083	Diptera		Diptera		0,605	2
210	Dip084	Diptera		Diptera		0,447	1
211	Dip085	Diptera		Diptera		0,017	1
212	Dip086	Diptera		Diptera		0,229	1
213	Dip087	Diptera		Diptera		0,192	1
214	Dip088	Diptera		Diptera		1,039	4
215	Dip089	Diptera		Diptera		6,221	1
216	Dip090	Diptera		Diptera		0,679	9
217	Dip091	Diptera		Diptera		0,204	17
218	Dip092	Diptera		Diptera		0,281	8
219	Dip093	Diptera		Diptera		0,781	1
220	Dip094	Diptera		Diptera		0,534	2
221	Dip095	Diptera		Diptera		0,102	1
222	E001	Ephemeroptera		Tourist		1,287	17
223	Hem001	Hemiptera	Pentatomidae	Herbivore	Sucker	3,096	93
224	Hem002	Hemiptera	Pentatomidae	Herbivore	Sucker	10,901	29
225	Hem003	Hemiptera	Fulgoridae	Herbivore	Sucker	2,719	5
226	Hem004	Hemiptera	Fulgoridae	Herbivore	Sucker	0,967	7
227	Hem005	Hemiptera	Fulgoridae	Herbivore	Sucker	0,670	1
228	Hem006	Hemiptera	Reduviidae	Predator		0,165	35
229	Hem009	Hemiptera	Issidae	Herbivore	Sucker	0,681	8
230	Hem010	Hemiptera	Miridae	Herbivore	Sucker	0,406	7
231	Hem012	Hemiptera	Psyllidae	Herbivore	Sucker	0,209	12
232	Hem014	Hemiptera	Delphacidae	Herbivore	Sucker	0,242	5
233	Hem016	Hemiptera	Anthocoridae	Predator		0,166	29
234	Hem017	Hemiptera	Anthocoridae	Predator		0,113	65

235	Hem019	Hemiptera	Lygaeidae	Herbivore	Sucker	0,509	229
236	Hem025	Hemiptera	Cercopidae	Herbivore	Sucker	2,317	1
237	Hem028	Hemiptera	Membracidae	Herbivore	Sucker	2,090	2
238	Hem029	Hemiptera	Derbidae	Herbivore	Sucker	0,648	29
239	Hem031	Hemiptera	Ciccadellidae	Herbivore	Sucker	0,682	4
240	Hem032	Hemiptera	Psyllidae	Herbivore	Sucker	0,659	1
241	Hem033	Hemiptera	Ciccadellidae	Herbivore	Sucker	0,263	2
242	Hem035	Hemiptera	Psyllidae	Herbivore	Sucker	0,218	206
243	Hem036	Hemiptera	Scutelleridae	Herbivore	Sucker	0,911	82
244	Hem037	Hemiptera	Psyllidae	Herbivore	Sucker	0,084	37
245	Hem038	Hemiptera		Herbivore	Sucker	0,030	2
246	Hem039	Hemiptera	Fulgoridae	Herbivore	Sucker	0,496	1
247	Hem040	Hemiptera	Lygaeidae	Herbivore	Sucker	0,659	3
248	Hem041	Hemiptera	Lygaeidae	Herbivore	Sucker	0,035	1
249	Hem042	Hemiptera	Lygaeidae	Herbivore	Sucker	0,191	1
250	Hem043	Hemiptera	Tingidae	Herbivore	Sucker	0,232	24
251	Hem044	Hemiptera	Pyrrhocoridae	Herbivore	Sucker	0,826	5
252	Hem046	Hemiptera	Saldidae	Predator		0,073	1
253	Hem047	Hemiptera	Pentatomidae	Herbivore	Sucker	35,697	6
254	Hem049	Hemiptera	Lygaeidae	Herbivore	Sucker	0,356	24
255	Hem050	Hemiptera	Ciccadellidae	Herbivore	Sucker	1,831	5
256	Hem051	Hemiptera	Ciccadellidae	Herbivore	Sucker	0,400	2
257	Hem052	Hemiptera	Ciccadellidae	Herbivore	Sucker	1,231	1
258	Hem053	Hemiptera	Ciccadellidae	Herbivore	Sucker	0,575	1
259	Hem054	Hemiptera	Anthocoridae	Predator		0,044	1
260	Hem055	Hemiptera	Delphacidae	Herbivore	Sucker	0,136	1
261	Hem058	Hemiptera	Tingidae	Herbivore	Sucker	0,348	1
262	Hem062	Hemiptera	Lygaeidae	Herbivore	Sucker	22,755	1
263	Hem063	Hemiptera	Pentatomidae	Herbivore	Sucker	13,048	3
264	Hem064	Hemiptera	Ciccadellidae	Herbivore	Sucker	3,038	1
265	Hem065	Hemiptera	Pentatomidae	Herbivore	Sucker	0,102	3

266	Hem066	Hemiptera	Lygaeidae		Herbivore	Sucker	0,275	1
267	Hem068	Hemiptera	Coreidae		Herbivore	Sucker	16,642	9
268	Hem070	Hemiptera	Lygaeidae		Herbivore	Sucker	0,502	3
269	Hem071	Hemiptera	Alydidae		Herbivore	Sucker	20,461	1
270	Hem072	Hemiptera	Ciccadellidae		Herbivore	Sucker	0,278	1
271	Hem075	Hemiptera	Fulgoridae		Herbivore	Sucker	1,238	3
272	Hem076	Hemiptera	Ciccadellidae		Herbivore	Sucker	2,838	1
273	Hem077	Hemiptera	Ciccadellidae		Herbivore	Sucker	1,293	5
274	Hem078	Hemiptera	Coreidae		Herbivore	Sucker	9,784	1
275	Hem079	Hemiptera	Ciccadellidae		Herbivore	Sucker	0,162	2
276	Hem082	Hemiptera	Ciccadellidae		Herbivore	Sucker	1,073	3
277	Hem083	Hemiptera	Pentatomidae		Herbivore	Sucker	39,047	1
278	Hem084	Hemiptera	Ciccadellidae		Herbivore	Sucker	2,619	2
279	Hem085	Hemiptera	Ciccadellidae		Herbivore	Sucker	2,386	2
280	Hem086	Hemiptera	Ciccadellidae		Herbivore	Sucker	1,412	1
281	Hem087	Hemiptera	Fulgoridae		Herbivore	Sucker	1,213	1
282	Hem089	Hemiptera	Ciccadellidae		Herbivore	Sucker	1,032	2
283	Hem090	Hemiptera	Pentatomidae		Herbivore	Sucker	1,545	4
284	Hem091	Hemiptera			Herbivore	Sucker	0,097	1
285	Hem092	Hemiptera	Ciccadellidae		Herbivore	Sucker	1,188	1
286	Hem093	Hemiptera	Ciccadellidae		Herbivore	Sucker	0,622	1
287	Hem094	Hemiptera	Pentatomidae		Herbivore	Sucker	4,771	1
288	Hym001	Hymenoptera	Formicidae	*Mesoponera* sp.	Formicidae		0,308	35
289	Hym002	Hymenoptera	Formicidae	*Linepithema humile*	Formicidae		0,074	427
290	Hym003	Hymenoptera	Formicidae	*Tetraponera emeryi*	Formicidae		0,119	60
291	Hym004	Hymenoptera	Formicidae	*Monomorium* sp.	Formicidae		0,028	43
292	Hym005	Hymenoptera	Formicidae	*Tetraponera clypeata*	Formicidae		0,259	16
293	Hym006	Hymenoptera	Formicidae	*Crematogaster liengmei*	Formicidae		0,205	283
294	Hym007	Hymenoptera	Formicidae	*Camponotus* sp. *1*	Formicidae		2,019	5
295	Hym009	Hymenoptera	Apidae		Pollinator		26,052	2
296	Hym010	Hymenoptera			Parasitoid		0,111	5

297	Hym011	Hymenoptera			Parasitoid	4,518	1
298	Hym012	Hymenoptera			Parasitoid	3,197	1
299	Hym013	Hymenoptera			Parasitoid	0,400	1
300	Hym014	Hymenoptera			Parasitoid	0,853	1
301	Hym015	Hymenoptera			Parasitoid	0,197	55
302	Hym016	Hymenoptera			Parasitoid	0,442	34
303	Hym017	Hymenoptera			Parasitoid	0,086	2
304	Hym018	Hymenoptera			Parasitoid	0,129	1
305	Hym019	Hymenoptera			Parasitoid	0,168	3
306	Hym020	Hymenoptera			Parasitoid	0,198	5
307	Hym021	Hymenoptera			Parasitoid	0,668	6
308	Hym022	Hymenoptera			Parasitoid	0,117	33
309	Hym023	Hymenoptera			Parasitoid	0,157	2
310	Hym024	Hymenoptera			Parasitoid	0,522	7
311	Hym025	Hymenoptera			Parasitoid	0,295	2
312	Hym026	Hymenoptera			Parasitoid	0,074	2
313	Hym027	Hymenoptera			Parasitoid	0,196	2
314	Hym028	Hymenoptera			Parasitoid	0,160	6
315	Hym029	Hymenoptera			Parasitoid	0,065	1
316	Hym030	Hymenoptera			Parasitoid	0,468	6
317	Hym031	Hymenoptera			Parasitoid	0,255	12
318	Hym032	Hymenoptera			Parasitoid	0,061	1
319	Hym033	Hymenoptera			Parasitoid	0,133	2
320	Hym034	Hymenoptera			Parasitoid	0,041	1
321	Hym035	Hymenoptera			Parasitoid	0,116	30
322	Hym036	Hymenoptera			Parasitoid	0,014	1
323	Hym037	Hymenoptera			Parasitoid	0,032	39
324	Hym038	Hymenoptera			Parasitoid	0,050	3
325	Hym039	Hymenoptera	Formicidae	*Tapinoma* sp. *1*	Formicidae	0,018	37
326	Hym041	Hymenoptera			Parasitoid	0,424	1
327	Hym042	Hymenoptera			Parasitoid	0,540	1

328	Hym043	Hymenoptera			Parasitoid	0,894	3
329	Hym044	Hymenoptera			Parasitoid	0,144	1
330	Hym045	Hymenoptera			Parasitoid	0,562	1
331	Hym046	Hymenoptera			Parasitoid	0,217	1
332	Hym047	Hymenoptera			Parasitoid	2,380	7
333	Hym048	Hymenoptera			Parasitoid	1,324	1
334	Hym050	Hymenoptera			Parasitoid	0,377	1
335	Hym051	Hymenoptera			Parasitoid	0,042	1
336	Hym053	Hymenoptera			Parasitoid	0,017	1
337	Hym054	Hymenoptera			Parasitoid	0,662	2
338	Hym055	Hymenoptera			Parasitoid	4,073	1
339	Hym056	Hymenoptera			Parasitoid	0,442	3
340	Hym057	Hymenoptera			Parasitoid	0,089	3
341	Hym058	Hymenoptera			Parasitoid	0,532	1
342	Hym059	Hymenoptera			Parasitoid	0,258	3
343	Hym060	Hymenoptera			Parasitoid	0,319	1
344	Hym062	Hymenoptera			Parasitoid	1,131	1
345	Hym063	Hymenoptera			Parasitoid	0,083	2
346	Hym064	Hymenoptera			Parasitoid	0,055	4
347	Hym065	Hymenoptera			Parasitoid	0,384	1
348	Hym066	Hymenoptera			Parasitoid	0,243	2
349	Hym067	Hymenoptera			Parasitoid	0,198	8
350	Hym068	Hymenoptera			Parasitoid	0,033	1
351	Hym069	Hymenoptera			Parasitoid	0,095	7
352	Hym070	Hymenoptera			Parasitoid	0,387	1
353	Hym071	Hymenoptera			Parasitoid	0,184	1
354	Hym072	Hymenoptera			Parasitoid	0,023	2
355	Hym073	Hymenoptera			Parasitoid	0,191	1
356	Hym074	Hymenoptera	Formicidae	*Lepisiota capensis* subsp. *minuta*	Formicidae	0,039	2
357	Hym075	Hymenoptera			Parasitoid	0,059	2
358	Hym076	Hymenoptera			Parasitoid	0,020	5

359	Hym077	Hymenoptera			Parasitoid	0,309	7
360	Hym078	Hymenoptera			Parasitoid	0,073	1
361	Hym079	Hymenoptera			Parasitoid	0,026	1
362	Hym080	Hymenoptera			Parasitoid	0,009	1
363	Hym081	Hymenoptera			Parasitoid	0,205	1
364	Hym082	Hymenoptera			Parasitoid	0,335	1
365	Hym083	Hymenoptera			Parasitoid	0,119	3
366	Hym084	Hymenoptera			Parasitoid	0,539	1
367	Hym085	Hymenoptera			Parasitoid	0,004	1
368	Hym086	Hymenoptera			Parasitoid	0,006	6
369	Hym087	Hymenoptera	Formicidae	*Tapinoma* sp. *2*	Formicidae	0,015	1
370	Hym088	Hymenoptera			Parasitoid	0,040	29
371	Hym089	Hymenoptera			Parasitoid	7,391	2
372	Hym090	Hymenoptera			Parasitoid	0,104	6
373	Hym091	Hymenoptera			Parasitoid	0,044	1
374	Hym092	Hymenoptera			Parasitoid	0,092	1
375	Hym093	Hymenoptera	Formicidae	*Pheidole tenuinodis*	Formicidae	0,275	1
376	Hym094	Hymenoptera			Parasitoid	1,144	1
377	Hym095	Hymenoptera			Parasitoid	0,037	1
378	Hym096	Hymenoptera			Parasitoid	0,312	4
379	Hym097	Hymenoptera			Parasitoid	0,073	2
380	Hym098	Hymenoptera			Parasitoid	0,009	1
381	Hym099	Hymenoptera	Apidae		Pollinator	33,487	1
382	Hym100	Hymenoptera			Parasitoid	0,324	1
383	Hym101	Hymenoptera			Parasitoid	0,234	5
384	Hym102	Hymenoptera			Parasitoid	0,043	1
385	Hym103	Hymenoptera			Parasitoid	0,031	2
386	Hym104	Hymenoptera			Parasitoid	0,029	1
387	Hym105	Hymenoptera			Parasitoid	0,106	3
388	Hym106	Hymenoptera			Parasitoid	0,178	1
389	Hym107	Hymenoptera			Parasitoid	0,384	1

390	Hym108	Hymenoptera			Parasitoid		0,280	1
391	Hym109	Hymenoptera			Parasitoid		0,121	3
392	Hym110	Hymenoptera			Parasitoid		0,068	1
393	Hym111	Hymenoptera			Parasitoid		0,593	1
394	Hym112	Hymenoptera			Parasitoid		0,077	1
395	Hym113	Hymenoptera	Formicidae	*Leptogenys* sp.	Formicidae		0,278	4
396	Hym114	Hymenoptera			Parasitoid		0,144	2
397	Hym115	Hymenoptera	Formicidae	*Myrmicaria nigra*	Formicidae		1,156	8
398	Hym116	Hymenoptera			Parasitoid		0,124	3
399	Hym117	Hymenoptera			Parasitoid		0,048	1
400	Hym118	Hymenoptera			Parasitoid		0,131	1
401	Hym119	Hymenoptera	Formicidae	*Technomyrmex* sp.	Formicidae		0,051	1
402	Hym120	Hymenoptera			Parasitoid		0,451	2
403	Hym121	Hymenoptera			Parasitoid		0,099	1
404	Hym122	Hymenoptera	Vespidae		Predator		19,124	1
405	Hym123	Hymenoptera			Parasitoid		11,440	1
406	Hym124	Hymenoptera	Pompilidae		Predator		11,415	1
407	Hym125	Hymenoptera			Parasitoid		0,543	1
408	Hym126	Hymenoptera			Parasitoid		0,053	2
409	Hym127	Hymenoptera	Formicidae	*Camponotus* sp. *2*	Formicidae		0,278	2
410	Iso001	Isopoda			Detritivore		0,577	4
411	J001	Archaeognatha			Detritivore		0,371	2
412	K001	Psocoptera			Detritivore		0,075	26
413	K002	Psocoptera			Detritivore		0,078	173
414	K003	Psocoptera			Detritivore		0,145	91
415	K004	Psocoptera			Detritivore		0,022	12
416	K005	Psocoptera			Detritivore		0,022	232
417	La001	Neuroptera	Chrysopidae	Larvae	Predator		0,520	16
418	La002	Lepidoptera	Geometridae	Larvae	Herbivore	Chewer	2,235	1
419	La003	Neuroptera	Chrysopidae	Larvae	Predator		0,390	5
420	La004	Coleoptera	Carabidae	Larvae	Predator		0,249	2

421	La005	Coleoptera	Coccinellidae	Larvae	Predator		0,727	5
422	La006	Coleoptera	Coccinellidae	Larvae	Predator		0,718	4
423	La007	Coleoptera	Coccinellidae	Larvae	Predator		0,248	7
424	La009	Coleoptera	Carabidae	Larvae	Predator		0,028	4
425	La010	Coleoptera	Coccinellidae	Larvae	Predator		0,162	5
426	La011	Lepidoptera	Geometridae	Larvae	Herbivore	Chewer	3,085	3
427	La013	Hemiptera	Aphididae	Larvae	Herbivore	Sucker	0,212	3
428	La016	Lepidoptera	Geometridae	Larvae	Herbivore	Chewer	2,763	1
429	La018	Lepidoptera		Larvae	Herbivore	Chewer	0,564	2
430	La019	Lepidoptera	Geometridae	Larvae	Herbivore	Chewer	7,029	2
431	La021	Neuroptera	Chrysopidae	Larvae	Predator		0,544	4
432	Lepi001	Lepidoptera			Pollinator		1,465	3
433	Lepi002	Lepidoptera			Pollinator		0,649	9
434	Lepi003	Lepidoptera	Zygaenidae		Pollinator		16,175	2
435	Lepi004	Lepidoptera	Noctuidae		Pollinator		6,064	1
436	Lepi005	Lepidoptera			Pollinator		0,561	1
437	Lepi008	Lepidoptera			Pollinator		1,082	1
438	Mant001	Mantodea	Mantidae		Predator		2,909	1
439	Mant002	Mantodea	Mantidae		Predator		1,223	1
440	Mant003	Mantodea	Mantidae		Predator		0,436	1
441	N001	Neuroptera	Chrysopidae		Pollinator		0,512	6
442	N002	Neuroptera	Chrysopidae		Pollinator		0,635	2
443	N003	Neuroptera			Pollinator		0,053	1
444	O001	Orthoptera	Gryllidae		Herbivore	Chewer	25,630	13
445	O002	Orthoptera	Gryllidae		Herbivore	Chewer	3,828	1
446	O003	Orthoptera	Stenopelmatidae		Herbivore	Chewer	6,184	1
447	O004	Orthoptera	Stenopelmatidae		Herbivore	Chewer	0,589	1
448	Od001	Odonata	Coenagrionidae	*Pseudagrion kersteni*	Predator		292,679	1
449	P001	Pseudoscorpiones			Predator		NA	79
450	P002	Pseudoscorpiones			Predator		NA	18
451	P003	Pseudoscorpiones			Predator		NA	3

452	P004	Pseudoscorpiones		Predator		NA	7
453	Phasma001	Phasmatodea	Phasmatidae	Herbivore	Chewer	47,614	9
454	ST001	Amphipoda		Detritivore		3,778	12
455	T001	Acari		Predator		NA	11
456	T002	Acari		Predator		NA	6
457	T003	Acari		Detritivore		NA	12
458	T004	Acari		Detritivore		NA	4
459	T005	Acari		Predator		NA	89
460	T006	Acari		Predator		NA	23
461	T007	Acari		Predator		NA	21
462	T008	Acari		Predator		NA	27
463	T009	Acari		Herbivore	Chewer	NA	1
464	T010	Acari		Predator		NA	3
465	T011	Acari		Predator		NA	5
466	T012	Acari		Parasitoid		NA	2
467	T013	Acari		Predator		NA	1
468	Ty001	Thysanoptera	Thripidae	Herbivore	Sucker	0,350	64
469	Ty002	Thysanoptera	Thripidae	Herbivore	Sucker	0,036	17
470	Ty003	Thysanoptera	Thripidae	Herbivore	Sucker	0,016	16
471	Ty004	Thysanoptera	Thripidae	Herbivore	Sucker	0,107	1
472	V001	Dermaptera	Forficulidae	Detritivore		5,849	2
473	V002	Dermaptera	Forficulidae	Detritivore		0,290	1

NA: Excluded from biomass analyses due to model constraints

Chapter 3

No home-field advantage in leaf litter decomposition in an ancient temperate rainforest system despite selective detritivore responses toward different tree species

Abstract

The home-field advantage (HFA) hypothesis states that leaf litter decomposes more rapidly beneath plant species from which the leaves originate (home environment), than under other plant species. Most HFA studies typically involve reciprocal litter transplants between habitat types (i.e. forest vs. grassland) or successional stages (i.e. early vs. late). However, studies on HFA rarely assess this phenomenon within a single ecosystem between numerous source tree species in mixed forests, i.e. at the tree species scale. Also, only few studies directly assess detritivore diversity in terms of HFA reciprocal litter transplants. This is despite homogenous litter build up close to any given tree individual in a mixed forest, along with evidence of varying decomposition rates under different plant species driven by host selection by fungi as well as detritivores. To address these gaps, we firstly determined differences in decomposition rates between leaves of three dominant forest tree species. Hereafter we compared decomposition rates between home plots (beneath source trees) and away plots (beneath different tree species) in a mixed-tree natural, temperate rainforest. We used litterbags of two mesh sizes and different chemical treatments to partition the relative contribution of detritivorous arthropod biota (both meso- and macrofauna) from overall decomposition rates and that by fungi (microbiota). We also assessed detritivore arthropod diversity of each treatment. We give evidence that leaf-litter decomposition rates can differ significantly depending on the source-tree species. Despite this, we found no HFA in terms of decomposition of leaf litter under source trees, as opposed to trees of other species. Only one tree species showed differences in arthropod diversity between home and away plots. Furthermore, arthropods here contributed significantly more than fungi to overall decomposition. However, bacteria (not measured here) may also have decomposed litter greatly, as ca. 20% of litter loss was not due to our focal groups. We conclude that, in a single, diverse forest, perhaps due to differences in litter fall rate and nutrient content of leaf litter, only some species might reveal HFA patterns for detritivores, with yet unknown effects on decomposition HFA. Our results indicate that HFA is not evident at the tree species scale within a natural mixed forest system.

Keywords: Decomposition; detritivore; home-field advantage; leaf litter

Introduction

Decomposition is an important ecological process in forest habitats, especially for cycling nutrients (Aerts 1997). Between 60-90% of terrestrial primary production is decomposed in the soil (Giller 1996), contributing greatly to the global carbon cycle, yet it is vulnerable to global climate change (Aerts 1997; Houghton 2007). Leaf litter breakdown begins with activity by detritivore macrofauna, such as earthworms, woodlice, and millipedes (Swift et al. 1979; Fragoso and Lavelle 1992), along with mesofauna, including mites and springtails (Kurzatkowski et al. 2004). The shredded leaf litter then enables microbiota to reduce the organic fragments into basic molecules (Lavelle et al. 1993).

Variation in decomposition rates between different systems is largely dependent on climate, litter quality, and the decomposer community (Coûteaux et al. 1995). Climate acts through effects on metabolism by bacteria and fungi (Swift et al. 1979; Aerts 1997), in addition to affecting leaf litter production, including variations in leaf quality and chemistry (Lill and Marquis 2001). Litter quality and chemistry is a major determinant of the decomposition process (Strickland et al. 2009; Bradford et al. 2016; Schilling et al. 2016), with local tree species diversity affecting litter mass reduction (Jewell et al. 2015). Together, climate and litter quality explains <70% variation in the decomposition process, with ca. 30% of remaining variation due to less well-defined parameters (Ayres et al. 2009a).

About 4-8% of leaf litter breakdown has been attributed to home-field advantage (HFA) (Gholz et al. 2000; Ayres et al. 2006, 2009a). The HFA hypothesis states that leaf litter decomposes more rapidly beneath plant species from which the leaves originate (home environment), compared to environments with different plant species. Studies on HFA typically involve reciprocal litter transplants between habitat types (i.e. forest vs. grassland) or successional stages (i.e. early vs. late), and subsequently assess relative effect of similarity or dissimilarity between leaf litter and local environment (Ayres et al. 2009a). Although HFA has been described from different forests globally (Ayres et al. 2009a), it is still a contentious topic, with patterns seemingly strongly context dependent, impeding its incorporation into ecological theory (Freschet et al. 2012). For example, no HFAs have been detected in subtropical forests in China (Wu et al. 2019), northern Arizona (Chapman and Koch 2007), or from forests-grasslands in New Zealand (St. John et al. 2011). Furthermore, explanatory mechanisms for HFA patterns and processes are poorly understood, with the relative roles of microbiota and mesofauna in this process only starting to be deciphered (Austin et al. 2014; Lin et al. 2019).

Reciprocal litter transplant techniques used in HFA studies are often undertaken in ecosystems with high ecological contrast (Veen et al. 2018; Freschet et al. 2012), with disparate litter qualities, or which include forest ecosystems with certain plant species dominating (Ayres et al. 2009b). HFA studies rarely assess this phenomenon within a single ecosystem between numerous source tree species in mixed forests (Gießelmann et al. 2011). This is despite evidence suggesting that plant species identity within an ecosystem greatly affects decomposition. Effect of plant species on decomposition has been suggested in a temperate Patagonian forest (Vivanco and Austin 2008), and a tropical French Guiana tropical forest (Hättenschwiler et al. 2008), with HFA and composition of decomposer communities being determined by source plant identity (Wardle et al. 2004; Bezemer et al. 2010).

In forest canopies, specialized herbivorous arthropods are physiologically adapted to the nutrient levels and chemical defences of particular host plants (Wardhaugh 2014). Such adaptations are an essential component of the resource concentration hypothesis (Futuyma and Wasserman 1980), where patterns in insect distribution, such as specialized herbivorous arthropods in forest canopies, reflect the distribution and availability of their preferred resource (Hamback and Englund 2005; Wardhaugh 2014). Similar to the canopy, the forest floor is not a homogenous mix of leaf species, with most leaves from an individual tree landing close by (Ferguson 1985). Among trees in a tropical Panama rainforest, leaves of species with the farthest drop reached distances of only 12 m from the trunk, with most species averaging <10 m (Donoso et al. 2010). Leaf litter local distribution and resource preference and specialization by decomposers (Hansen 1999) are therefore suggested as a basis for the HFA hypothesis (Long et al. 2003).

Both macro- and mesofauna may significantly affect HFA (Milcu and Manning 2011). However, the effect of detritivorous arthropods (Bultman and Uetz 1984; Pramanik et al. 2001) has received little attention in HFA studies. Furthermore, studies that include mesofauna often show disparate results (Supplementary material, table S1), despite experimentation isolating the effect of detritivorous arthropods, and even distinguishing between macro- and mesofauna through altering litterbag mesh sizes (Bradford et al. 2002).

Some saprophytic arthropods forage specifically on leaf litter (Illig et al. 2008). Furthermore, where there is specificity among soil microbes according to tree species, arthropod microbivores may also vary, and would appear adapted to different types of leaf litter (Grove 2002; Donoso et al. 2010). Although often regarded as generalists (Scheu and Setala 2002; Wardle 2005; Ayres et al. 2006), decomposers are often affected by plant identity (Wardle et al. 2004; Vivanco and Austin 2008; Bezemer et al. 2010). Macrofauna, for example, greatly affect decomposition relative to source tree species (Riutta et al. 2012). In turn, secondary decomposing mesofauna, such as mites, can be more specialized than primary decomposing microbiota like fungi and bacteria (St. John et al. 2011).

Microbiota, such as saprophytic fungi, often specialize on their substrates, and are high in functional diversity (Kubatová et al. 2009; McGuire et al. 2010). Predictably then, within diverse natural forest systems, with a wide variety of substrates, phenomena such as HFA should tend toward tree species-level specialization (Gießelmann et al. 2011). However, ability of soil microbiota to use litter types of different quality is important for decomposition, and probably determined by past resource input (Strickland et al. 2009), suggesting that HFA is partly driven by soil microbiota detecting differences in chemical properties between leaf litter types (Perez et al. 2013). Furthermore, fungi might contribute to HFA through specific fungal community composition associated with faster rates of decomposition at ‘home’ sites (Lin et al. 2019), with certain dominant fungi dictating HFA patterns (Veen et al. 2019). Additionally, arbuscular mycorrhizal fungi, through local adaptation, could also create novel interactions between plants and soils, affecting HFA processes (Rúa et al. 2016). However, to date the relative contribution to HFA by soil macro-, meso- and microbiota is still poorly understood, despite their various yet important functional roles (Bardgett 2005), their reliance on leaf litter for nutrients and energy (Wardle 2002), and being relatively diverse in forest ecosystems (Stork and Grimbacher 2006).

To the best of our knowledge, the HFA hypothesis has yet to be explored in a single, diverse temperate rainforest system between different local source tree species while also including a direct assessment of the soil fauna involved. In England, pure stands of three tree species did not lead to a specialized decomposer community at the source species-level (Ayres et al. 2006). However, their study did not include larger soil fauna, meaning that further work under field conditions is required to include a broad range of soil biota, and bearing in mind that plant species create specific conditions enhancing the detrital community to breakdown species-specific litter (Vivanco and Austin 2008). In a diverse tropical forest, HFA might occur among individual tree species, leading to small-scale litter mosaics, with associated specialized decomposing communities (Gießelmann et al. 2011).

Here we determine whether there are differences in the decomposition rates between leaves of three dominant forest tree species using mesh bags containing single-species leaf litter. We used litterbags of two mesh sizes and different chemical treatments to decipher the relative contribution of fungal (re: microbiota) and detritivorous arthropod biota (both meso- and macrofauna) towards overall decomposition rates. We also compare decomposition rates between mesh bags placed underneath trees from which bag leaves derive (home) and trees of different species (away), expecting that the resource concentration hypothesis would explain any HFA patterns at the tree species scale. To explore the possible role of macro- and mesofauna in possible HFA, we determined whether there are differences in richness of decomposer taxa and/or their assemblage composition between home and away plots. We aim to determine the existence of, and driving forces behind, HFA within small, isolated forest habitats.

Materials and Methods

Study site

Southern Afro-temperate forests represent the largest forest complex in South Africa, characterised by high plant diversity of tropical affinity (Von Breitenbach 1974). Southern Afro-temperate forests are particularly interesting as they largely escaped the ice sheets during recent glacial maxima (Clark et al. 2009), and therefore have had longer evolutionary timeframes than most northern temperate forests to engage in numerous mutualisms (Geldenhuys 1993; Aizen and Ezcurra 1998). Also, numerous different tree species (<47 species) can dominate the canopy layer (Geldenhuys 1993). Moreover, the taxon ratio between species and genera is 1.5, which is lower than southern Brazilian rainforests and most northern and southern temperate forests (Berliner 2009), making most tree species phylogenetically isolated within their natural habitat. All these characteristics raise expectations of high interspecific specificity between individual tree species and the various organisms associated with them, including the decomposers. These forests have a naturally disjunct distribution along the southern and eastern coast of the country (Geldenhuys 1994). Here, we focus on one of these forest patches, Oubos, on the southern slopes of the Riviersonderend mountain range on nutrient poor, well-drained, sandy soils (-34.07S, 19.83E) in the Western Cape Province, South Africa. Oubos comprises an area of 381 ha at the western boundary of the southern Afro-temperate forests, and receives rain year round, averaging ± 1000 mm annually. These forests, despite being comprised mostly of evergreen trees, can attain annual leaf litter fall rates of over 4 500 kg/ha/yr in moist areas, whereas standing litter mass can be over 8500 kg/ha and up to 12 500 kg/ha (Geldenhuys and Theron 1994).

Litterbag preparation

We chose three focal tree species that are dominant in southern Afro-temperate forests (Geldenhuys 1993): *Olea capensis macrocarpa*, *Podocarpus latifolius* and *Rapanea melanophloeos*. The first species, *O. c. macrocarpa* (Oleaceae), is an evergreen tree with fairly large (<150 mm) and stiff, leathery leaves. It is a medium to very large, late successional species that can attain a height of <35 m in mature forests with long and straight trunks (Venter 2011). The second species, *P. latifolius* (Podocarpaceae), is an evergreen gymnosperm, with stiff, narrow and leathery leaves (<80 mm). It can attain heights of <33 m in mature forests, with straight and long stems (Von Breitenbach 1985; Venter 2011). Finally, *R. melanophloeos* (Myrsinaceae), is a small to large evergreen tree, which can attain heights of <25 m in mature forests, with straight and cylindrical trunks (Von Breitenbach 1985). Its leaves are thick and leathery (<140 mm) (Venter 2011).

In 2017, senescent leaves were collected from these species at Oubos forest. Collected leaves were air dried for two months, in a sunlit laboratory, in open brown paper bags, and then oven-dried for 48 hrs at 55°C. This temperature is suggested as suitable from a previous study, and avoids heat-induced breakdown of most leaf chemical compounds (Makkar and Singh 1991).

Mesh litterbags are often used to assess decomposition rates, and, using differences in mesh size and chemical treatments, certain decomposing biota can be excluded. Litterbags were constructed of nylon mesh, double layered, and were 15 cm × 15 cm in size. All litterbags had fine mesh (<0.5 mm) as a bottom layer (the layer that was in contact with the soil) to prevent larger leaf litter fragments, which were not considered decomposed in our study, from falling through. The top layer of the litterbags consisted of either coarse mesh (1.5 mm) to allow for movement of macro- and mesofauna into the bags (Kampichler and Bruckner 2009), or fine mesh to exclude macrofauna, but include microarthropods which have lower body size limits of 0.02 mm (Illig et al. 2008; Kampichler and Bruckner 2009). All bags were filled with exactly 5 g dried leaf litter of a single tree species.

In addition to the fine mesh/ coarse mesh treatments, litterbags of each size class were also treated with either fungicide (to prevent fungal colonization) or naphthalene (to deter arthropod colonization). Naphthalene, a polycyclic aromatic hydrocarbon ($C_{10}H_8$) is an effective chemical deterrent of arthropods (Soong et al. 2016), and has a negligible effect on soil microbial abundance (Cotrufo et al. 2014). For the prevention of fungal growth, we used a broad spectrum fungicide containing metalaxyl as active ingredient. While fungicide treatment of leaves currently has a contentious effect on the colonization of litter by other microbes (e.g. bacteria, Møller et al. 1999; Yang et al. 2011) and, predictably, a negligible effect on macro- and mesofauna (Sayer et al. 2006), it does inhibit growth of most fungal taxa (Sayer et al. 2006). The fungicide was diluted following manufacturer recommendations, and litterbags treated with fungicide were submerged into the solution for 1 min, and then air dried prior to field placement. Bags not treated with fungicide were submerged in water and air dried before placement in the field. Bags earmarked for arthropod exclusion contained two naphthalene balls of 1.5 cm diameter. Negative control bags were not treated with any chemicals, and positive control bags were treated with both chemicals.

Sampling design

In total, 18 mature trees were selected in Oubos forest under which 'home-field' bags were placed (n = 6 individuals per species) at a minimum home inter-plot distance of 15 m. At home plots, all litterbags contained leaves of the same species as the home tree. An additional 18 away plots (trees) were also chosen (n = 6 individuals per tree species) at a minimum distance of 20 m from home trees. At away plots, litterbags contained leaves of a different species from the tree species canopy overhead. Only individuals of the three focal tree species were selected so that each 'away' treatment contained two replicates of each source species. At each of the 36 plots ('home' and 'away' treatments), a total of eight leaf litterbags were placed (n = 288). These were placed at the corners of a 2 m x 2 m square around the base of the central tree, underneath its overlapping crown where litter accumulation is highest (Chomel et al. 2015). At each of the four corners, bags were placed in pairs (50 cm apart) according to the four chemical treatments (negative control, positive control, fungicide only treatment, naphthalene only treatment). Each litterbag in a pair at each corner had either fine mesh or coarse mesh as the top layer (Fig. 1), and were pinned to the forest floor using steel wire.

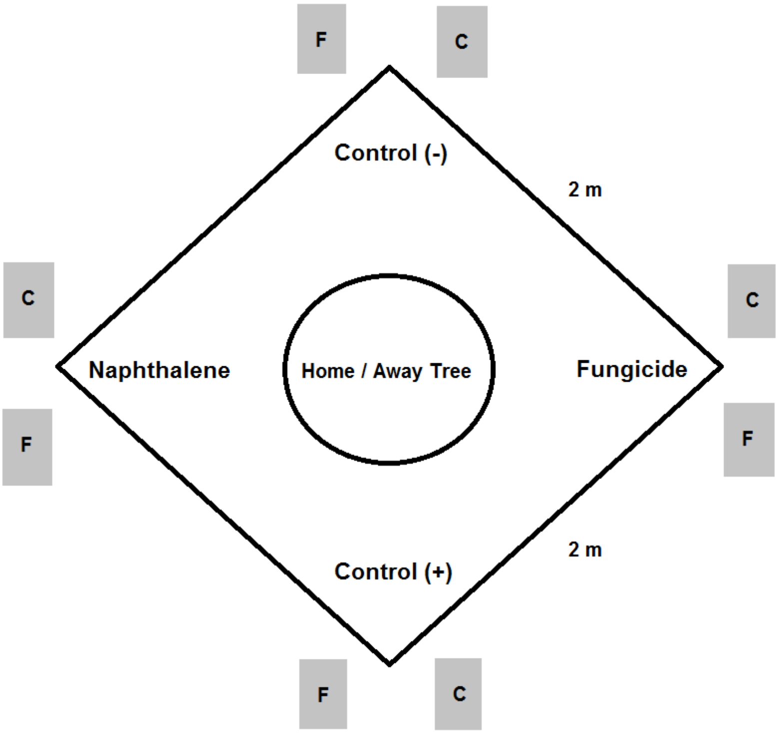

Figure 3: Plot layout indicating the placements of coarse mesh bags (C) and fine mesh bags (F) and the various chemical treatments and the positive (treated with both fungicide and Naphthalene) and negative (untreated) controls (n = 36 plots).

Data collection

Decomposition is fastest during the first 100 days, and decreases during winter (Portillo-Estrada et al. 2016). Therefore, litterbags were placed under the trees early August 2017, and collected after three months, early November 2017, spanning roughly 92 days. This time-period spanned the austral spring and early summer months, known for high arthropod activity in the region (Procheş and Cowling 2006), while also correlating with higher leaf litter arthropod diversity in other forests (Argyropoulou et al. 1993). This time also follows the winter months, during which litter fall is lowest for these forests, and marks the start of high rates of litter fall for most species during spring, reaching its peak in summer months (Geldenhuys and Theron 1994). Leaf-litter nitrogen levels also peak during spring and early summer in these forests (Geldenhuys and Theron 1994), which could affect arthropod activity.

Whereas previous HFA studies typically involve periods of litter exposure in the field of >6 months, we were particularly interested in the relationship between possible HFA and soil meso- and macrofauna, which largely initiates the early decomposition process for a wide array of detrital communities that follow. Two months of litterbag exposure time has been suggested to optimise arthropod colonisation (Prasifka et al. 2007), with leaf litter colonized by mites as early as 3 weeks after exposure (Stanton 1979), and even after several hours for millipedes (Lawrence and Samways 2002). We also attempted to decrease the amount of time for generalist, 'tourist' arthropods to enter leaf litterbags, which, predictably, increases with exposure time. Thus, to account for both optimal arthropod sampling and detection of litter breakdown rates, three months placement during spring and early summer were selected.

Each month, naphthalene balls were replenished, and fungicide was re-applied by spraying to ensure optimal concentrations of these chemicals to exclude arthropods and fungi. Litterbags were re-treated without removing them from the forest floor, and without disturbing their contents. After three months, litterbags were carefully lifted from the forest floor while ensuring no spillage of remaining contents (Coleman et al. 2017), and then placed in separate sealable plastic bags.

In the laboratory, litterbags were placed in a Berlese funnel, under 25W warm light bulbs (with the coarse side to the bottom where appropriate) to collect arthropods in ethylene glycol-filled tubes at the bottom of the funnels for 48 hrs (Edwards 1991; Sabu et al. 2011). Then the bags were removed and oven-dried for another 48 hrs at 70°C to a constant weight. Remaining litter was then carefully removed, and reweighed. The difference in weight between the initial 5 g and the weight after three months in the field represented total decomposition (Kaneko and Salamanca 1999). Percentage mass loss was determined for each bag, as only two weights were acquired during sampling, and therefore conventional linear regressions were not followed (Kaneko and Salamanca 1999; Vivanco and Austin 2008).

All sampled detritivorous arthropods were sorted to morphospecies, identified to the lowest possible taxonomic level, with each morphospecies being given a unique code (Labandeira 1997). Detritivores were classified according to the dietary intake for the particular taxonomic group of specific life stage collected (Scholtz and Holm 1985; Dindal 1990). These included not only arthropods that directly feed on plant litter, but also fungivores, microbivores, and omnivores, as these indirectly contribute to the removal of litter biomass via the microbes that colonise these substrates (Moore et al. 1988). A reference collection of all sampled arthropods is retained in the Entomology Museum, Stellenbosch University, South Africa (Supplementary material, table S2).

Statistical analyses

Decomposition

Decomposition data were transformed to a normal distribution using square-root transformation. The effect of the respective factors on decomposition were then determined through linear mixed-effect modelling (LMMs) using the *lme4* package in R (Bates *et al*. 2007). The model contained the factors ‘species’ (representing the source litter in the bags; *O. c. macrocarpa, P. latifolius, R. melanophloeos*), ‘location’ (either ‘home’ or ‘away’), ‘mesh size’ (either coarse or fine) and ‘treatment’ (chemical treatment as either the negative control (no chemical treatment), fungicide treatment, naphthalene treatment or positive control (treated with both chemicals)). Two-way interactions between all factors were included in the model. The individual tree under which bags were placed was included as a random variable in the model (Bolker et al. 2009). Pairwise differences in decomposition between significant factors were separated using a Tukey post-hoc using the *multcomp* package in R (Hothorn *et al*. 2008).

Arthropods

Both abundance and species richness data for detritivorous arthropods were overdispersed, and so generalized linear mixed-effect models (GLMMs) were constructed using the negative binomial distribution family using the package *glmmTMB* (Brooks et al. 2017). GLMMs for arthropod richness and abundance contained the same factors as those used for analyses of decomposition data. Pairwise differences in richness or abundance between significant factors were separated using a Tukey post-hoc test.

Assemblage compositional analyses were conducted using the *manyglm* function in the *mvabund* package using R software (Wang et al. 2012). Abundance data were used, best modelled here with the negative binomial distribution family, with all factors mentioned before included in the full model. This package also considers all interactions between factors. Results were visually presented using the function *lvsplot* in the *boral* package in R (Hui 2016; Warton et al. 2015). This follows a Bayesian model-based approach and accounts for residual correlation by incorporating pure latent variables, in unconstrained analyses, and environmental variables, in constrained analyses (Hansen et al. 2016). This is especially useful for overdispersed data, as the distribution family, for example negative binomial, can be selected.

Results

Decomposition

Source species (litter identity), chemical treatment, and mesh size had significant effects on litter breakdown (Table 1). Location (home vs. away) had no significant effect on decomposition. Furthermore, no interactive effects were detected between these variables. Of the three source species, leaves of *R. melanophloeos* decomposed much faster (ca. 35% mass loss) than those of *O. c. macrocarpa* and *P. latifolius* (ca. 23% mass loss), which were similar to one another (Fig. 2A). In terms of chemical treatment, bags that allowed the inclusion of arthropods (i.e. negative control bags and those treated with fungicide) had significantly higher mass loss than those where these were excluded (positive control bags and those treated with naphthalene) (Fig. 2B). Mass loss did not differ between negative control bags (untreated bags) and those treated with fungicide (fungal exclusion) (Fig. 2B). Similarly mass loss did not differ between positive control bags (exclusion of fungi and arthropods) and those treated with naphthalene (arthropod exclusion). Litterbags covered with coarse mesh, that allowed both micro- and macro-arthropods access to litter, had higher decomposition (ca. 28%) than those covered with fine mesh (ca. 24%), which only allowed micro-arthropods access to leaf litter (Fig. 2C).

Table 1: Results of linear modelling (LMMs) showing the effects of source species (litter identity), litterbag location (home or away), chemical treatment and mesh size, as well as their interactions, on leaf litter decomposition (% mass loss). Reported χ^2-values.

Factor	***df***	**Chi-square**
Source species	2	**146.04*****
Location	1	0.04
Chemical treatment	3	**33.81*****
Mesh size	1	**29.21*****
Source species × location	2	1.16
Source species × chemical treatment	6	4.85
Source species × mesh size	2	2.10
Location × chemical treatment	3	3.78
Location × mesh size	1	1.31
Chemical treatment × mesh size	3	5.24

* P < 0.05, **P < 0.01, ***P < 0.001

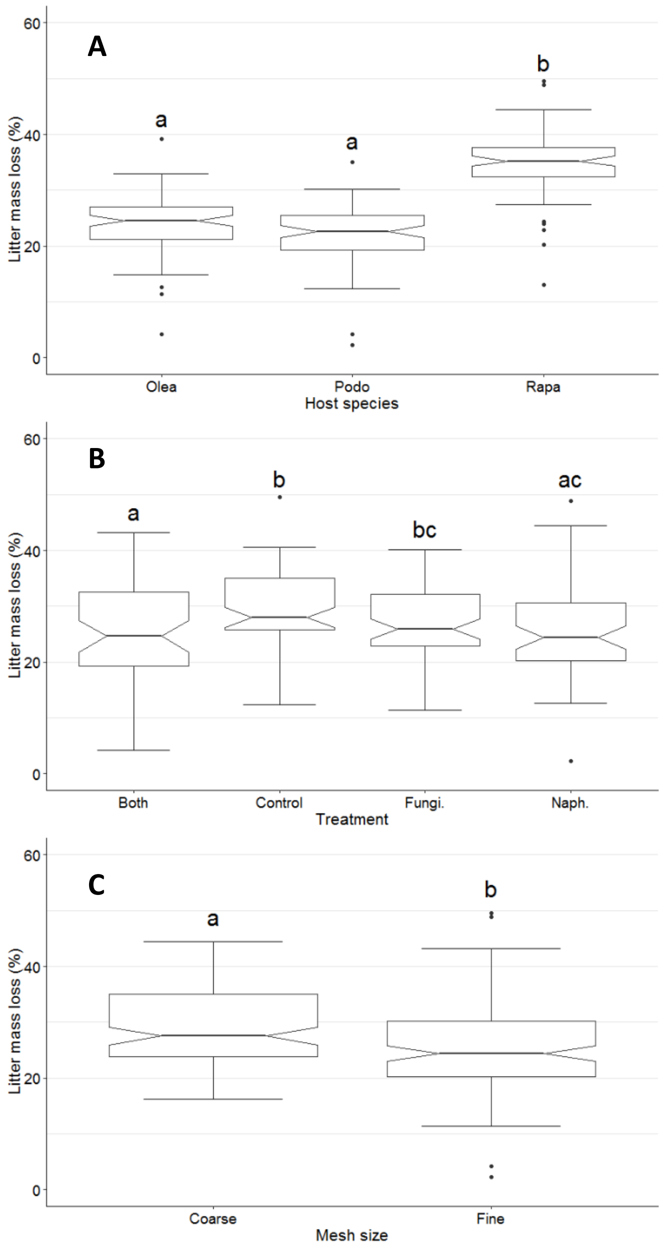

Figure 2: Boxplot of differences in mean percentage litter mass loss over the study period between (A) the three selected source tree species, (B) the four chemical treatments, and (C) the two mesh sizes. Different letters above bars indicate significantly different means based on a Tukey post-hoc test. Olea = *O. c. macrocarpa;* Podo = *P. latifolius;* Rapa = *R. melanophloeos*. Naph. = naphthalene treated bags, Fungi. = fungicide treated bags, Control = negative control (no chemicals), Both = positive control (treated with both chemicals). Box indicates 25%-75% data range, and whiskers indicate minimum and maximum values.

Arthropods

A total of 81 detritivorous arthropod species were sampled from litterbags. Species richness was estimated at 109 (SD ± 14) using Chao2 and 122.82 using Jacknife2. Forty detritivorous arthropod species were sampled from *O. c. macrocarpa*, with Chao2 estimating 61.13 (SD ± 16.43) species and Jacknife2 estimating 61.66. From *P. latifolius*, 46 detritivorous arthropod species were sampled, with Chao2 estimating 86.5 (SD ± 28.55) species, and Jacknife2 estimating 77.41. From *R. melanophloeos*, 62 detritivorous arthropod species were sampled, with Chao2 estimating 80.18 (SD ± 10.69) species and Jacknife2 estimating 90.67.

Chemical treatment and mesh size had a significant effect on detritivore abundance and species richness (Table 2). Bags to which arthropods had access (negative controls and those treated with fungicide) had the highest abundance and richness, and did not differ from each other (Figs. 3A and 4A). Those treated with naphthalene (including the positive control) had lowest detritivore richness and abundance, which also did not differ statistically (Figs. 3A and 4A). Although the difference in medians were small, bags covered in coarse mesh contained higher species richness and abundance than those covered with fine mesh (Figs. 3B and 4B).

The interactive effect of source species and location was significant for detritivorous arthropod species richness and their abundance (Table 2). This was largely due to higher species richness and abundance of detritivores when litter of *R. melanophloeos* was placed under trees of this species (home field plots), while other species did not differ much in terms of richness or abundance at home or away plots (Figs. 3C and 4C). Chemical treatment and mesh size also had a significant interactive effect, but only in terms of detritivore species richness (Table 2). This was due to a decrease in the effect of arthropod non-exclusion (negative controls and bags treated with fungicide) on detritivore richness in the bags covered by the fine mesh as opposed to the ones that were covered in the coarse mesh (Fig. 4D).

Table 2: Results of generalized linear mixed-effect modelling (GLMMs) showing the effects of source species, litterbag location (home or away), chemical treatment, and mesh size on detritivore abundance and species richness, as well as on the interactions between these factors. Reported χ^2-values.

Response variable	**Factor**	***Df***	**Chi-square**	**(P)>Chi-square**
Abundance	Source species	2	4.26	0.12
	Location	1	0.94	0.33
	Chemical treatment	3	38.82	**< 0.001*** **
	Mesh size	1	6.81	**0.01** **
	Source species × location	2	6.89	**0.03***
	Source species × chemical treatment	6	7.36	0.29
	Source species × mesh size	2	0.78	0.68
	Location × chemical treatment	3	1.31	0.73
	Location × mesh size	1	0.94	0.33
	Chemical treatment × mesh size	3	7.06	0.07
Species richness	Source species	2	4.008	0.1348
	Location	1	0.78	0.38
	Chemical treatment	3	33.88	**< 0.001*** **
	Mesh size	1	12.92	**< 0.001*** **
	Source species × location	2	7.47	**0.02***
	Source species × chemical treatment	6	8.73	0.21
	Source species × mesh size	2	0.6	0.74
	Location × chemical treatment	3	3.8	0.28
	Location × mesh size	1	1.96	0.16
	Treatment × mesh size	3	9.11	**0.03***

* P < 0.05, **P < 0.01, ***P < 0.001

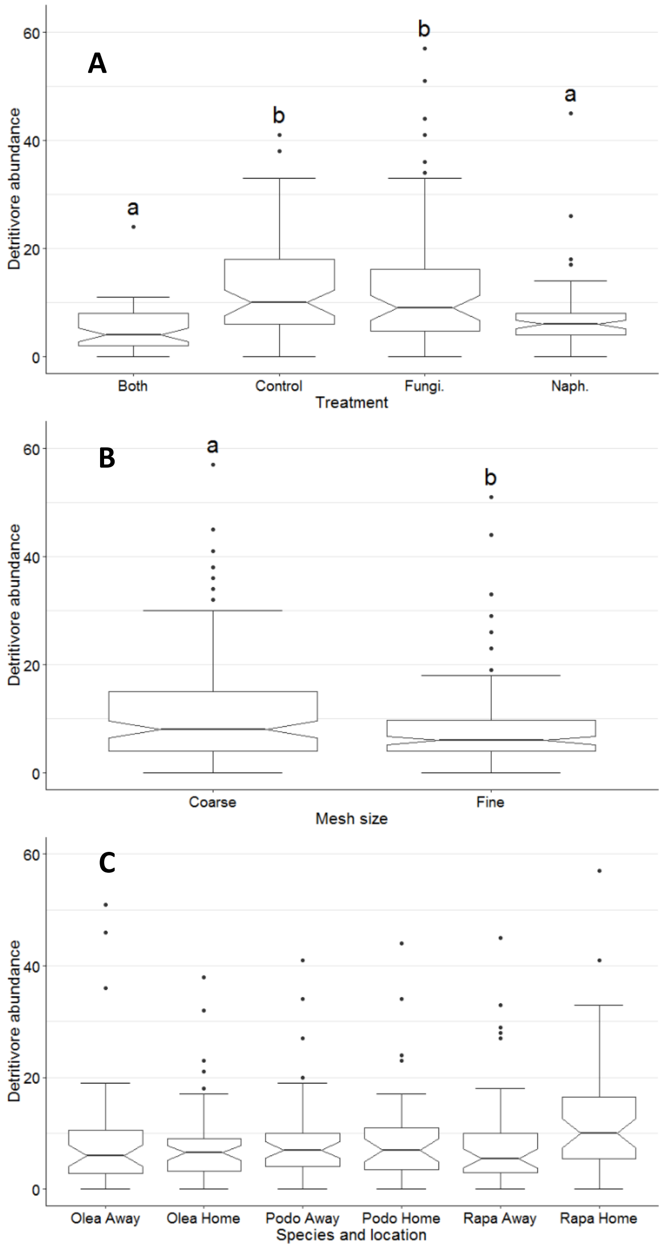

Figure 3: Boxplot of differences in detritivore abundance sampled from litterbags between (A) the four chemical treatments, (B) the two mesh sizes and (C) between the two locations for each of the source species. Different letters above bars indicate significantly different medians based on a Tukey post-hoc test. Naph. = naphthalene treated bags; Fungi. = fungicide treated bags; Control = negative control (no chemicals); Both = positive control (treated with both chemicals). Box indicates 25%-75% data range, whiskers indicate minimum and maximum values.

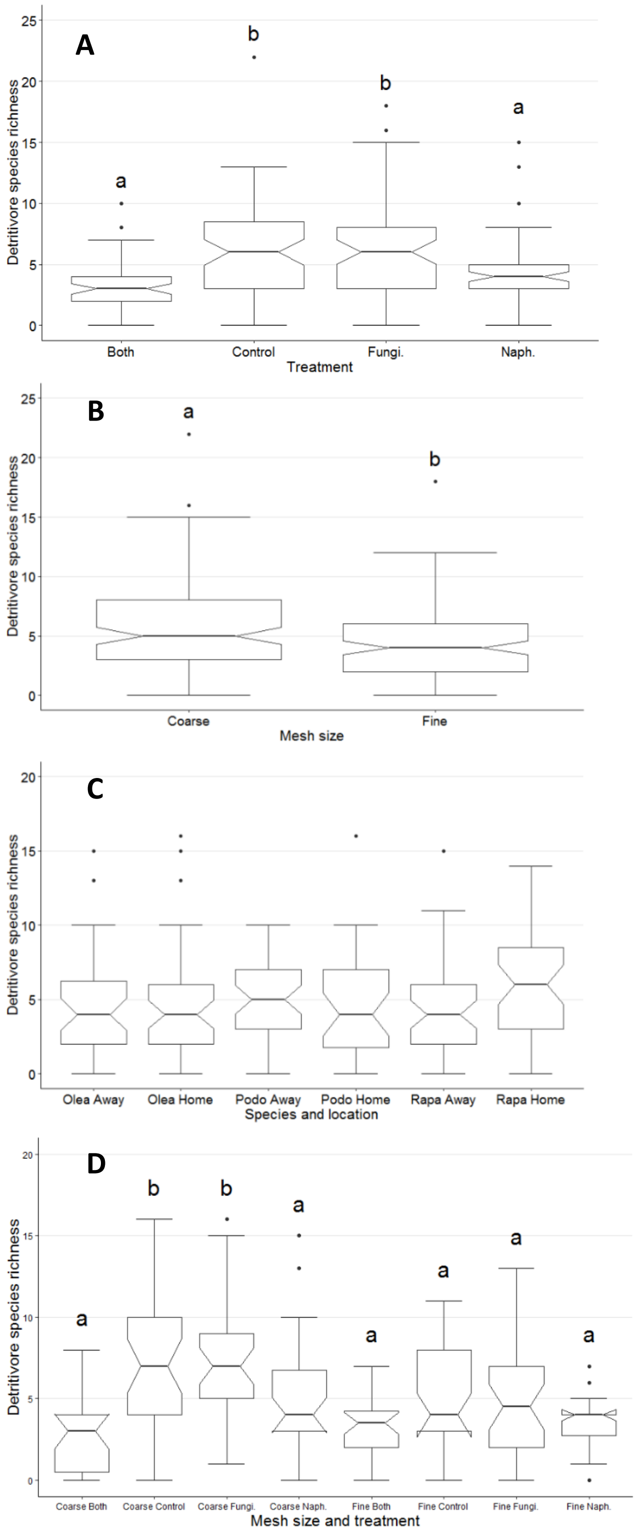

Figure 4: Boxplot of differences in detritivore species richness sampled from litterbags between (A) the four chemical treatments, (B) the two mesh sizes, (C) the two locations for each of the source species, and (D) the two mesh sizes for each of the four treatments. Different letters above bars indicate significantly different medians based on a Tukey post-hoc test. Naph. = naphthalene treated bags, Fungi. = fungicide treated bags. Box indicates 25%-75% data range, and whiskers indicate minimum and maximum values.

Detritivorous arthropod assemblage composition differed significantly in comparisons between source species, chemical treatments, and mesh sizes (Table 3). Location (home or away) did not affect detritivorous arthropod assemblage composition (Table 3). Detritivore assemblage composition associated with *O. c. macrocarpa* leaf litter differed substantially from that associated with the other two source species, which, in turn, were similar (Fig. 5). One species, M8 (Oribatida: Ceratozetidae) (Supplementary material, table S2), for example, was commonly associated with *O. c. macrocarpa* leaves, with an abundance of 56 for species M8 on leaf litter of *O. c. macrocarpa*, compared to the other tree species, which had 12 (*P. latifolius*) and 14 (*R. melanophloeos*) individuals. Although *R. melanophloeos* shared many detritivorous taxa with the other tree species, higher abundance of these generalist taxa was often found among its leaf litter (Supplementary material, table S2). This was true especially for the order Sarcoptiformes (Supplementary material, table S2). As expected, detritivore assemblage composition of treatments that allowed arthropod access to litter differed substantially from those that excluded arthropods, but detritivore assemblage composition for negative control bags (untreated) and bags treated with fungicide only, did not differ markedly (Fig. 5). Interactive effects of source species and location were significant (Table 3), mostly through detritivore assemblages being associated with *R. melanophloeos* (Supplementary material, fig. S3). In addition, the interactive effects of chemical treatment and location, and chemical treatment and mesh size, were also significant (Table 3).

Table 3: Results of the assemblage compositional analyses using multivariate generalised linear modelling showing the effects of source species, litterbag location (home or away), chemical treatment, and mesh size, and their two-way interactions on the assemblages of the detritivorous arthropods.

Factor	***Df***	**Dev.**	**P**
Source species	2	283	**0.001*** **
Location	1	103	0.056
Chemical treatment	3	390	**0.001*** **
Mesh size	1	170	**0.001*** **
Source species × location	2	127	**0.001*** **
Source species × chemical treatment	6	202	0.118
Source species × mesh size	2	79	0.085
Location × chemical treatment	3	161	**0.003** **
Location × mesh size	1	38	0.325
Chemical treatment × mesh size	3	161	**0.001*** **

* P < 0.05, **P < 0.01, ***P < 0.001

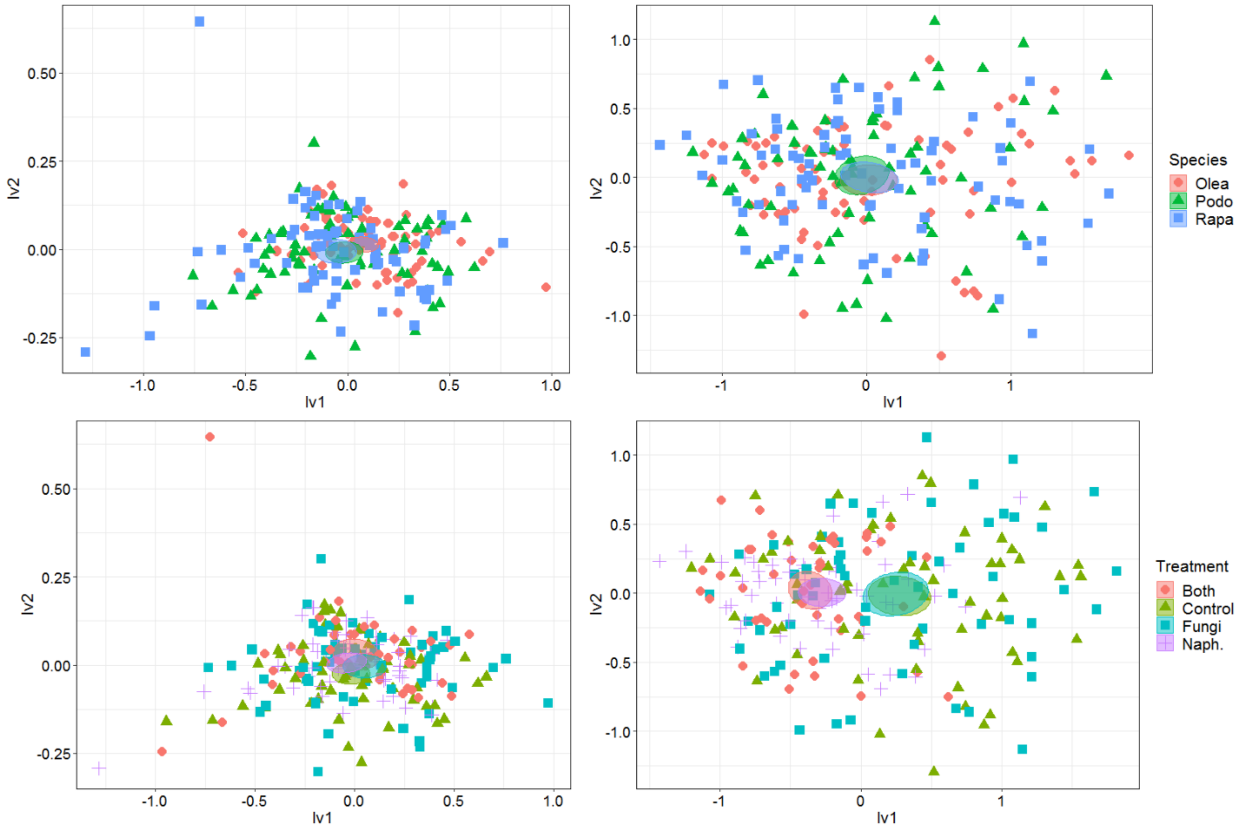

Figure 5: Bayesian ordination analysis of multivariate abundance data showing composition similarity of detritivorous arthropods with (left) an unconstrained latent variable model, and (right) a constrained latent variable model considering source tree species in the top figures and chemical treatment in the bottom figures using the boral package in R.

Discussion

This study was performed in a well-defined, single forest. Therefore, variations reported in decomposition rates and arthropod diversity cannot be ascribed to climatic variability, or soil properties, but rather to species specific or fine-scale location variability. We found no home-field advantage (HFA) in decomposition of leaf litter under source trees in this mixed-tree, southern Afro-temperate rainforest system and therefore reject the hypothesis that HFA is prevalent at the tree species-level scale. However, we found evidence that decomposition rates of leaf litter and arthropod assemblages can differ significantly depending on the source tree species. Furthermore, in accordance with other studies, arthropods here contributed significantly more than fungi to overall decomposition.

Different leaf litter types vary greatly in leaf size, shape, and nutrient levels (Ferguson 1985; Santiago 2007). Although all three species here have hard and leathery leaves, there are inter-specific differences in size and shape of leaves (Venter 2011). The studied species also have disparate evolutionary histories (Von Breitenbach 1974), likely driving large differences in leaf chemistry (Hättenschwiler et al. 2008). Surprisingly, the species that was phylogenetically most dissimilar (*P. latifolius*) was not the one that differed most in leaf decomposition rates, and was similar to that of *O. c. macrocarpa*. Rather, leaves of *R. melanophloeos*, a species phylogenetically more closely related to *O. c. macrocarpa*, were broken down much faster than those of the other two species. With the effect of climate accounted for here, differences in litter quality is likely the most significant factor in driving the observed differences in litter breakdown between the three studied species (Ayres et al. 2009b; Hansen 1999; Schilling et al. 2016). Indeed, among the three species here, *R. melanophloeos* leaves contain significantly higher levels of nitrogen than *P. latifolius*, and more than *O. c. macrocarpa* (unpublished data), which may have affected the detritivore community (Cuchietti et al. 2014).

Specialized herbivorous arthropods in forest canopies use volatiles to locate their host trees (Mithöfer et al. 2018), and actively disperse to preferred resource concentrations. Whether detritivorous arthropods can detect chemical differences in leaf litter type, especially in diverse and mixed forest floors, remains uncertain. Leaf litter emits volatile organic compounds (VOCs; Gray et al. 2010), and that VOCs have specific signatures, or olfactory cues, which millipedes, beetles, and oribatid mites use to recognize resources (Austin et al. 2014). Oribatid mites, the most abundant taxon here and in many other forest ecosystems (Laganiére et al. 2010), can move both passively on wind currents, as well as actively by walking and phoresy (Behan-Pelletier and Winchester 1998). Therefore, at least some movement might be directed towards specific resources, even when scattered across the landscape (Roets et al. 2009).

In Panamanian tropical forests, 12.5-33.3% of leaf litter invertebrates showed some specificity towards a given tree species, and a third of the oribatid mite species were leaf-litter specialists (Donoso et al. 2010). Here, in this ancient temperate rainforest, different tree species differed in their detritivore assemblage composition. However, the location of the leaves had no effect on detritivore assemblage composition. Therefore, leaf litter identity appears to have a filtering effect on the forest floor fauna, with leaves of specific sources attracting different arthropod assemblages regardless of proximity to source tree. For this to hold true, detritivorous arthropods must be able to detect their preferred resource within a heterogeneous leaf litter layer (Ferguson 1985; Austin et al. 2014).

Interestingly, *R. melanophloeos*, the species showing greatest litter mass loss, was also the species with greatest disparity in detritivore richness, abundance, and assemblage composition between home and away plots. Similar to St. John et al. (2011), we found no evidence to support leaf litter decomposition HFA, and therefore, we cannot imply that soil microbes-, meso- or macro-fauna form part of the explanatory mechanisms behind the process. Conversely, it is also not possible to imply that the unique detritivore patterns associated with *R. melanophloeos* are due to resource concentration, or HFA. Other factors, such as variation in forest leaf litter depth, which is greatest close to tree trunks, is partly due to short litter fall distances (Donoso et al. 2010), and leads to forest floor heterogeneity to which detritivores could adapt temporarily. Forest floor heterogeneity might also be driven by tree species having different rates of litter fall (Geldenhuys and Theron 1994). Here, monthly litter fall measurements revealed differences in amounts of litter fall between the three study species, with *R. melanophloeos* and *P. latifolius* regularly shedding leaves of >50 kg/ha compared to *O. c. macrocarpa* which only produces <40 kg/ha, and then only rarely so (Geldenhuys and Theron 1994). As such, reasons for the higher diversity at home sites for *R. melanophloeos* remain unclear, but likely include a combination of factors such as litter fall rates and leaf chemistry (Hansen and Coleman 1998; Bezemer et al. 2010; Laganiére et al. 2010; St. John et al. 2011).

As with the detritivorous arthropods, we found no evidence for HFA in terms of decomposition rates of leaves by fungi. As no differences were detected between leaf litterbags treated with fungicide and the control bags in terms of decomposition, it seems likely that fungi do not play a significant role in decomposition here, at least during the first 90 days of leaf litter breakdown. It is generally understood that soil detritivores act as shredders in the breakdown process, facilitating the initial breakdown of the leaves into smaller particles to be chemically reduced by bacteria and fungi (Aerts 1997), but also acting as a catalyst for subsequent microbial growth (Hansen 1999; Pramanik et al. 2001). It is therefore possible that more time was required to detect the action of fungal leaf litter breakdown here. Also, we found high levels of decomposition in litterbags treated with both fungicide and naphthalene, albeit less than in the control bags. Possibly, microbes such as bacteria or natural, resistant fungi, here play significant roles in litter breakdown, as bags treated with naphthalene and fungicide still had decomposition levels of over 20%.

In Canada, the greater the litter dispersal capability of a tree species, the less pronounced is HFA (Chomel et al. 2015). Importantly, this hypothesis is built around extents of leaf mixing, with species with greater litter-dispersal capabilities encouraging leaf mixture. This might have led to the detrital community adapting to various sources over a single one, thereby decreasing HFA (Chomel et al. 2015). Leaf mixing in southern Afro-temperate forests is relatively high not only due to, predictably, diverse litter dispersal capacities between the <47 canopy species (which were not tested here), but also due to a diverse, largely intermingled and dense tree crown, encouraging the mixture of leaf litter. Moreover, the Cape region is characterized by strong seasonal winds, and southern Afro-temperate forests are largely restricted to high southern mountain slopes (Geldenhuys 1994). Generally, wind intensity increases with increases in elevation (Brown et al. 2011), perhaps further leading to high levels of leaf mixing. As such, HFA effects are likely less pronounced within a single, mixed tree forest system, partially due to high levels of leaf litter mixing, as opposed to between different systems, although more work is needed in other old-growth forests.

In conclusion, HFA is not a prevalent phenomenon within southern Afro-temperate forests at the tree species scale. However, different source tree species do show differences in leaf litter decomposition, and we show that within old-growth forest systems, different source species might show greatly differing patterns in detritivore arthropod diversity. We suggest that leaf litter of a single tree species is not necessarily viewed by detritivores as small-scale homogenous patches beneath plants of origin (Gießelmann et al. 2011). Instead, leaves are detected regardless of proximity to leaf origin in high diversity forests, with predictably high rates of leaf litter mixing. However, certain species within a diverse forest, perhaps those with higher litter fall rates and more nutritious leaves, could create small-scale homogenous patches for detritivorous arthropods to exploit. As such, we predict that where HFA occurs within a system, it should be species-dependent. Species-dependency might be the case in our system due to the opportunity for a long association, and therefore adaptation, between arthropods and trees at least throughout the Neogene, and during which, there have been no severe climatic events such as glaciation or volcanism. Alternatively, detritivores show little specialisation in the leaf type they consume, perhaps due to highly diverse and mixed litter layers. Conditions promoting HFA are still poorly understood, as evidence seems context-dependent, and universal patterns remain vague (Veen et al. 2015; Lin et al. 2019). We recommend that future studies of HFA in natural forest ecosystems take into account the detritivorous arthropod assemblage, but also couple this with a longer time frames than the current study to also account for fluctuations in decay rate (Prescott 2005) and seasonality (Sun and Zhao 2016). Lastly, it is possible that HFA and similar cryptic phenomenon are strong drivers of forest biodiversity through niche specialization (Devictor et al. 2010), with yet unresolved effects on the broader forest ecosystem functioning (Ayres et al. 2009a; Milcu and Manning 2011).

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Supplementary material

Table S1: Summary of recent home-field advantage (HFA) publications that included meso- and/or macrofauna in their analyses, together with the main findings pertaining to the included fauna.

Publication	**Habitat**	**Method**	**Time left in field**	**Soil fauna**	**Findings**
Gießelmann et al. 2011	Three successional stages of Atlantic rainforest, Brazil	Reciprocal litter transplant between forest successional stages	6 months	Macro- and meso-invertebrates	No HFA. Macro- and meso-invertebrates play a minor role in decomposition.
Milcu & Manning 2011	Three successional stages ranging from recently tilled, mature grassland and deciduous forest, Southeast England	Reciprocal litter transplant between 3 successional stages	12 months	Earthworms and mesofauna	HFA for 2 late successional stages. Mesofauna stimulates HFA.
St. John et al. 2011	Historically grazed grassland and mono-dominant forest, New Zealand	Reciprocal litter transplant between grassland and forest	9 months	Mites	No HFA. Mites show strong habitat specificity, but no litter specificity.
Chomel et al. 2015	Spruce and poplar forests, including mixed plantations, Canada	Reciprocal litter transplant between 2 mono-specific and 1 mixed plantation	7, 11, 18, 24 month intervals	Detritivorous microarthropods and predators	Greater mite abundance in spruce plantations. Spruce HFA possibly linked to detritivorous mites and springtails.
Gergócs & Hufnagel 2016	Microcosms of oak, pine and black locust leaves sampled from 3 woodland types, Hungary	Microcosms inoculated with 'home' and 'foreign' mesofauna	Half after 3 months, and other half after 12 months	Collembola, oribatid mites and other mites	Origin of mesofauna important for pine mass loss only. Litter quality better explains patterns in decay rate than HFA.
Asplund et al.	European beech and Norway spruce forests, Norway	Reciprocal litter transplant between 2 forest types	11 months	Mites and Collembola	Litter identity affects both mite and springtail

al. 2017					abundance. No HFA for either group.
Lin et al. 2019	Three forest types, including broadleaf, coniferous and bamboo, subtropical China	Reciprocal litter transplant of leaves from dominant tree species in each forest type	222 days (± 7 months)	Soil meso- and macrofauna through mesh size exclusion	HFA detected for broadleaf and bamboo litter. No effect of soil fauna on HFA.

Table S2: Morphospecies list for sampled detritivorous arthropods from leaf litter of three forest species with lowest taxonomic classification, total abundance and life stage.

Morpho Code	**Class**	**Subclass**	**Order**	**Suborder**	**Family**	***O. c. macrocarpa***	***P. latifolius***	***R. melanophloeos***	**Total**	**Life stage**
M3	Arachnida	Acari	Oribatida		Ceratozetidae	89	64	122	275	Adult
M5	Arachnida	Acari	Oribatida		Ceratozetidae	42	42	49	133	Adult
M8	Arachnida	Acari	Oribatida		Ceratozetidae	56	12	14	82	Adult
M32	Arachnida	Acari	Oribatida		Phthiracaridae	0	1	0	1	Adult
M4	Arachnida	Acari	Oribatida		Phthiracaridae	132	102	100	334	Adult
M1	Arachnida		Sarcoptiformes			34	38	58	130	Adult
M10	Arachnida		Sarcoptiformes			45	48	77	170	Adult
M11	Arachnida		Sarcoptiformes			4	2	9	15	Adult
M12	Arachnida		Sarcoptiformes			19	26	37	82	Adult
M14	Arachnida		Sarcoptiformes			0	0	2	2	Adult
M17	Arachnida		Sarcoptiformes			1	0	4	5	Adult
M18	Arachnida		Sarcoptiformes			15	2	5	22	Adult
M2	Arachnida		Sarcoptiformes			63	58	112	233	Adult
M24	Arachnida		Sarcoptiformes			15	9	22	46	Adult
M25	Arachnida		Sarcoptiformes			0	0	1	1	Adult
M27	Arachnida		Sarcoptiformes			0	1	1	2	Adult

M28	Arachnida		Sarcoptiformes		0	0	1	1	Adult
M33	Arachnida		Sarcoptiformes		3	0	0	3	Adult
M34	Arachnida		Sarcoptiformes		0	2	0	2	Adult
M35	Arachnida		Sarcoptiformes		0	1	0	1	Adult
M7	Arachnida		Sarcoptiformes		14	16	28	58	Adult
M9	Arachnida		Sarcoptiformes		17	8	11	36	Adult
ISO17	Diplopoda				0	1	0	1	Adult
LA23	Diplopoda				0	0	1	1	Adult
LA27	Diplopoda				1	1	0	2	Adult
ISO2	Entognatha	Collembola	Entomobryomorpha		39	32	46	117	Adult
ISO3	Entognatha	Collembola	Entomobryomorpha		17	10	29	56	Adult
ISO4	Entognatha	Collembola	Entomobryomorpha		1	1	6	8	Adult
ISO1	Entognatha	Collembola	Poduromorpha	Poduridae	54	45	66	165	Adult
ISO7	Entognatha	Collembola	Poduromorpha	Poduridae	0	0	2	2	Adult

ISO11	Entognatha	Collembola	Symphypleona	Sminthuridae	15	24	20	59	Adult
ISO12	Entognatha	Collembola	Symphypleona	Sminthuridae	0	0	2	2	Adult
ISO13	Entognatha	Collembola	Symphypleona	Sminthuridae	0	0	1	1	Adult
O6	Entognatha	Collembola	Symphypleona	Sminthuridae	1	0	0	1	Adult
ISO10	Entognatha	Collembola			0	0	3	3	Adult
ISO15	Entognatha	Collembola			0	1	1	2	Adult
ISO16	Entognatha	Collembola			0	0	1	1	Adult
ISO5	Entognatha	Collembola			0	0	2	2	Adult
MO1	Gastropoda				4	7	3	14	Adult
MO2	Gastropoda				0	0	2	2	Adult
MO3	Gastropoda				0	1	3	4	Adult

MO4	Gastropoda			16	16	15	47	Adult
MO5	Gastropoda			33	65	19	117	Adult
MO6	Gastropoda			1	10	17	28	Adult
MO7	Gastropoda			0	1	0	1	Adult
MO8	Gastropoda			0	3	0	3	Adult
MO9	Gastropoda			0	2	0	2	Adult
C8	Insecta	Coleoptera	Corylophidae	0	1	3	4	Adult
C19	Insecta	Coleoptera	Nitidulidae	0	1	1	2	Adult
C26	Insecta	Coleoptera	Nitidulidae	0	0	1	1	Adult
C39	Insecta	Coleoptera	Nitidulidae	1	0	0	1	Adult
C11	Insecta	Coleoptera	Ptiliidae	0	7	1	8	Adult
C23	Insecta	Coleoptera	Ptiliidae	0	0	1	1	Adult
C7	Insecta	Coleoptera	Scarabaeidae	2	0	5	7	Adult
C9	Insecta	Coleoptera	Scarabaeidae	0	4	8	12	Adult
C24	Insecta	Coleoptera	Tenebrionidae	0	2	0	2	Adult
C37	Insecta	Coleoptera	Tenebrionidae	1	0	0	1	Adult
C4	Insecta	Coleoptera	Tenebrionidae	0	0	1	1	Adult
C6	Insecta	Coleoptera	Tenebrionidae	0	0	2	2	Adult
D1	Insecta	Diptera		7	10	5	22	Adult

D10	Insecta	Diptera		0	1	0	1	Adult
D2	Insecta	Diptera		2	1	1	4	Adult
D3	Insecta	Diptera		1	1	2	4	Adult
D4	Insecta	Diptera		0	0	1	1	Adult
D5	Insecta	Diptera		0	0	2	2	Adult
D6	Insecta	Diptera		0	0	1	1	Adult
D7	Insecta	Diptera		0	0	1	1	Adult
D8	Insecta	Diptera		0	1	0	1	Adult
D9	Insecta	Diptera		0	1	0	1	Adult
K3	Insecta	Diptera		1	0	0	1	Adult
LA1	Insecta	Diptera		1	0	2	3	Larvae
LA11	Insecta	Diptera		0	0	1	1	Larvae
LA34	Insecta	Diptera		2	0	0	2	Larvae
LA5	Insecta	Diptera		1	0	3	4	Larvae
K1	Insecta	Psocoptera	Lachesillidae	3	5	12	20	Adult
K2	Insecta	Psocoptera	Psocidae	1	0	0	1	Adult
ISO9	Malacostraca	Amphipoda		0	0	10	10	Adult

CR1	Malacostraca	Isopoda	Oniscidea	0	0	12	12	Adult
CR2	Malacostraca	Isopoda	Oniscidea	1	13	2	16	Adult
LA2	Malacostraca	Isopoda	Oniscidea	2	0	1	3	Adult
LA4	Malacostraca	Isopoda	Oniscidea	0	0	2	2	Larvae

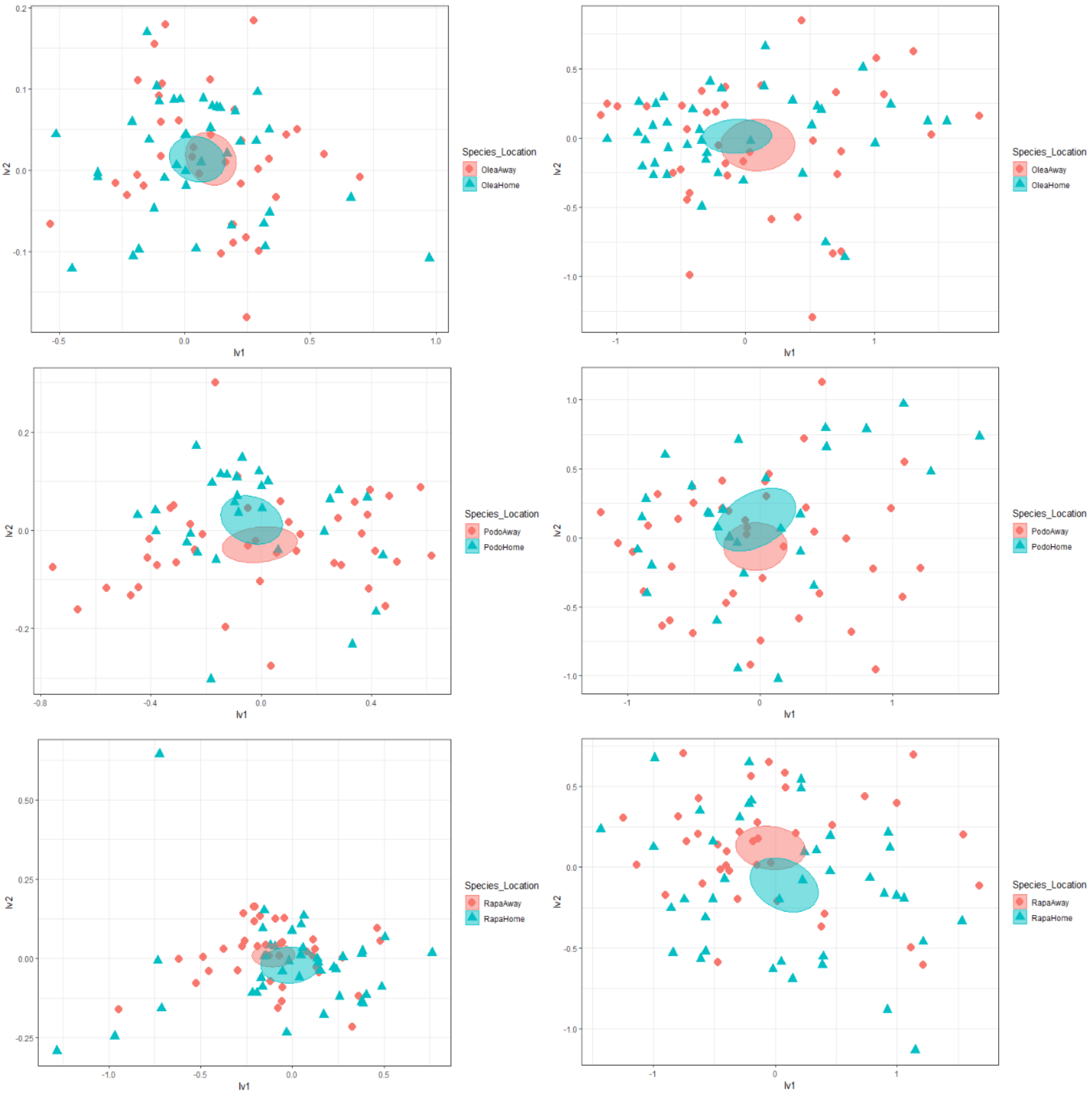

Figure S3: Bayesian ordination analyses of multivariate abundance data showing composition similarity of detritivorous arthropods for the interaction between source species and location with unconstrained latent variable models on the left, and constrained latent variable models, taking environmental variables into account, on the right using the *boral* package in R with the horizontal axes indicating latent variable 1 and the vertical axes indicating latent variable 2.

Chapter 4

Arthropods in Afrotemperate forest canopies reveal the unpredictability of biodiversity responses to environmental stressors

Abstract

Due to the large numbers of arthropod species captured at canopy level, many studies often focus on one arthropod taxonomic group or on a single tree species. A larger scale, multi-taxon approach is required to understand the subtle drivers of arthropod diversity in tree canopies. For example, the impact of the immediate surroundings around a tree individual on arthropod diversity remains understudied in forest canopies yet important. Changes in the surrounding environment may have profound effects on arthropod diversity, but also on plant physiological features. Precisely how changes in environmental factors influence plant characteristics and how arthropods respond to these changes is difficult to predict, as these may differ between plant species. Here, from numerous trees studied in southern Afrotemperate forests, I found that host tree identity was an important factor dictating arthropod diversity sampled from tree canopies, and that different tree species differ in many plant physiological variables. Also, I found a strong negative correlation between plot canopy cover and arthropod diversity. Here, most tree species showed some correlation between its physiology and associated arthropod diversity. Responses reported lacks clear patterns, with different tree species revealing different patterns. This confirms the complexity of how canopy arthropods perceive differences in tree species and individuals, and their physiology. I conclude that loss of single tree species, homogenization of the crown layer, and/or human-induced environmental change, could lead to great canopy community changes, threatening overall forest integrity.

Keywords: Arthropods, canopy, forest ecology, global change, tree-insect interactions

Introduction

Trees and their associated arthropods contribute greatly towards extant terrestrial biodiversity (Price 2002), with ecologists only recently begun to decipher the complexities of their interactions (Nakamura et al. 2017). This is because studies of arthropods in tree canopies are no longer severely hampered by challenges in accessibility (Adis et al. 1998); our understanding of arthropod communities (Dolek et al. 2009), their responses to different host tree species (Novotny & Basset 2005), and factors that influence their richness patterns (Basset et al. 2012), all of which are now better understood. This presents opportunities to investigate responses of tree canopy-associated arthropod diversity to more subtle factors in this ‘last biotic frontier’ (Erwin 1983; Bouget et al. 2011). For example, recent work has examined canopy arthropod feeding guild partitioning (Wardhaugh et al. 2012), incorporated evolutionary histories of host tree species (Arias et al. 2008), and investigated the effects of host-tree genetic diversity on arthropod diversity (Tovar-Sanchéz et al. 2015). However, how arthropod diversity in these little-known yet important ecosystems respond to novel, human-induced pressures, remains to be determined (Hallmann et al. 2017; Habel et al. 2019). Also, due to the large numbers of arthropod species captured at canopy level, many studies often focus on one arthropod taxonomic group (Allison et al. 1997; Sørensen 2004; Arias et al. 2008) or on a single tree species (Basset & Arthington 1992; Stork et al. 2001; Marques et al. 2006; Swart et al. 2019). As the multi-taxon approach provides deeper insights into ecological patterns and processes (Pryke & Samways 2012; Yekwayo et al. 2018), much of our earlier understanding regarding tree-insect interactions only applies to narrow contexts. A larger scale, multi-taxon approach is required to understand the subtle drivers of arthropod diversity in tree canopies.

Even though host specificity of arthropods in tree canopies is lower than previously thought (Novotny & Basset 2005; Mupepele et al. 2014), they are nevertheless likely to be at least as specialised as pollination networks in other systems (Wardhaugh et al. 2015). Host tree species identity is an important driver of arthropod diversity (Barone 1998; Allison *et al*. 1997), determined largely by differences in plant physiological features such as leaf size, chemical defences, turgor, and nitrogen content

(Wardhaugh 2014). However, the impact of the immediate surroundings around a tree individual on arthropod diversity remains understudied in forest canopies (Swart et al. 2019; Chapter 2).

In accordance with the resource concentration hypothesis, I expect higher abundance of a host tree species to maintain large numbers of specialized arthropods compared to trees surrounded by different species (Hamback & Englund 2005; Wardhaugh 2014). Similarly, large trees maintain high numbers of specialized arthropods (Grove 2002; Maeto et al. 2002; Campos et al. 2006), and denser foliage in canopies often host greater arthropod numbers (Dial et al. 2006). However, changes in the surrounding environment may also have profound effects on plant physiological features. When surrounded by dense canopies, a focal tree will receive less direct sunlight, which will decrease its photosynthetic capabilities and nutritional value (Knapp & Smith 1990). Changes in plant physiological features can also come about by factors such as drought, pollution, and changes in available nutrients (Grulke et al. 2002; Pollastrini et al. 2010). However, the influence of these subtle changes on arthropod diversity at tree canopy level is poorly studied (Maoela et al. 2018, 2019). This is concerning given that even a 1ºC increase in global temperature may have profound effects on the interactions between trees and arthropods (Kozlov et al. 2015). For example, decreased rainfall subject to global environmental change will lead to increased water stress, reduced growth, and subsequent disruptions of plant-arthropod dynamics in many areas (Ayres & Lombardero 2000; Bachelet *et al*. 2003; Lucht *et al*. 2006; Scholze *et al*. 2006; Lloyd & Bunn 2008; Allen *et al*. 2010). Other areas may experience increased forest vigour and growth, higher water use efficiency, and extended growing seasons (Ayres & Lombardero 2000; Bachelet *et al*. 2003; Lucht *et al*. 2006; Scholze *et al*. 2006; Lloyd & Bunn 2008; Allen *et al*. 2010). Precisely how changes in environmental factors influence plant characteristics and how arthropods respond to these changes is difficult to predict, as these may differ between plant species. Therefore, it is important to include factors such as tree stress-related factors and nutrient levels in canopy arthropod studies, especially over large biogeographical gradients (Pennings & Silliman 2005). This will then provide greater insight into how future climate change will shape tree canopy-arthropod interactions (Price et al.1980; López-Carretero et al. 2018; Renner & Zohner 2018) as it does for plant-pollinator interactions (Forrest 2015; Ponisio et al. 2017; Jauker et al. 2019; Hoiss et al. 2015).

Analysis of leaf physiology contributes to assessing various aspects of tree stress, such as moisture deficiency and nutrient status (Arndt et al. 2001). Foliar N concentration, in particular, is an important determinant of herbivore arthropod diversity, distribution, and feeding behaviour (Mattson 1980; Zehnder & Hunter 2009; White 2012; Hosseini et al. 2018), and may fluctuate from subtle changes in moisture availability (Heckathorn et al. 1997), pollution (Jones et al. 2008), and temperature (Chaitanya et al. 2001). Conversely, increased levels of foliar C often indicate plant investment towards anti-herbivory defences as structural compounds, phenols, and tannins (Huntly 1991; Chacón & Armesto 2006). Consequently, relative increases in foliar C/N ratio often indicate more allocation to carbon-based defences against herbivores (Gange & West 1994), which in turn also affects higher trophic levels (Paré & Tumlinson 1999). The investment plants make in producing these compounds is determined, for example, by level of exposure to light in both tropical (Denslow et al. 1990) and temperate (Dudt & Shure 1994) forests, as well as changes in environmental conditions such as drought, temperature, and pollution (Wolfenden et al. 1990; Heckathorn et al. 1997; Black et al. 2000). Drought-stress can lead to an increase in the relative metabolic uptake of $^{13}CO_{2,}$ (i.e. increased δ_{13}C) (Walker *et al*. 2015a; Arndt et al. 2001; Warren et al. 2001). In turn, variations in δ15N indicate differences in N sources (Evans 2001), for example, whether derived from the soil or atmosphere (Craine et al. 2015), while also indicating plant stress (Evans 2001) or exposure to pollution (Stewart et al. 2002). Response of canopy associated arthropod assemblages to changes in N and C isotopes can therefore provide valuable information regarding their responses to various stressors as predicted under future climate change (DeLucia et al. 2012).

Few studies have evaluated tree-arthropod interactions incorporating different tree species and the surrounding plot characteristics. Furthermore, I am unaware of any work that has examined how plot characteristics may affect the physiological features within individuals of a mix of different tree species in an indigenous Afromontane forest system, and how these changes might affect tree-associated arthropod diversity. I test three main hypotheses: 1) Tree identity and plot characteristics will affect arthropod diversity within canopies of focal trees, 2) Tree identity and plot characteristics will determine physiological features of focal trees, and 3) Arthropod diversity within canopies of particular host tree species will change according to within-host differences in tree physiological features. This study will therefore highlight important external influences, including stressors related to drought and differences in nutrient resources, on host tree physiology, and their impacts on canopy arthropod diversity.

Materials & Methods

Study area

The southern Afrotemperate forest complex represents the largest forests in South Africa and, although temperate in location, it has noticeable tropical affinities (Geldenhuys 1993). Indeed, many genera of tropical and subtropical origin (e.g. *Apodytes dimidiata*, *Diospyros whyteana*, *Kiggelaria africana*) are prominent components of southern Afro-temperate forests, and together with southern lineages such as *Cunonia*, *Podocarpus* and *Platylophus*, make up much of these forests (Geldenhuys 1993).

This study was conducted in five natural forests from Riviersonderend in the west (-34.04; 19.83) to Witelsbos in the east (-33.98; 24.11), in the southern Cape region of South Africa (Fig. 1). Southern Afrotemperate forests grow on nutrient-poor soils in areas that generally receive rain all year. Variations in nutrient availability for particular trees in forests might arise from differences in leaf litter nutrient release (Brearley et al. 2003), competition with other plants (Aerts 1999), and/or moisture availability (Garcia-Plazaola et al. 2008), especially in nutrient-poor soils. Average annual rainfall at my five study sites for the 5 years leading up to sampling (2012 – 2016) was 1003 mm, with no significant differences between sites. However, trees within the studied forests grow in areas that differ in soil moisture, largely due to differences in distance to small annual rivers, soil depth, and competition from diverse surrounding vegetation (Von Breitenbach 1974).

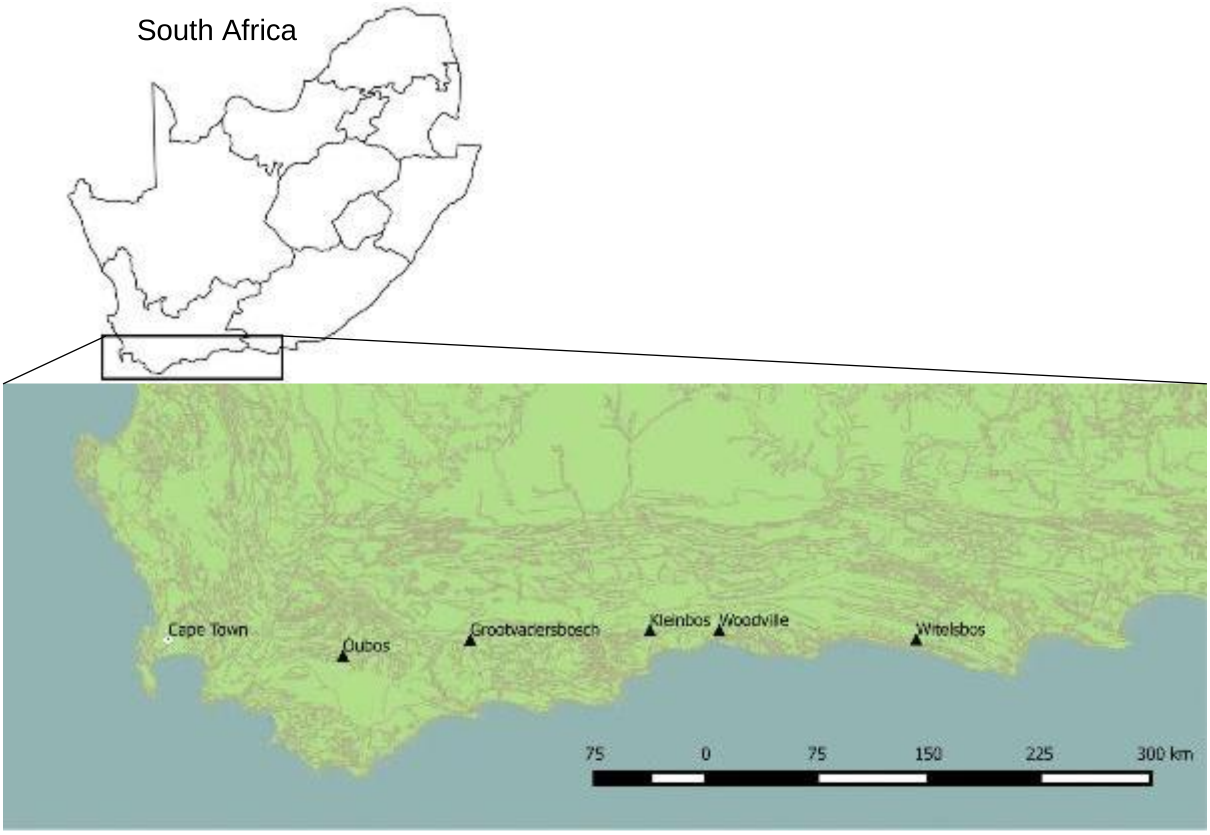

Figure 4: Study region in relation to South Africa, showing the five forests from which arthropods were sampled

Tree selection and arthropod collection

Eight focal tree species were selected (Table 1). Brief descriptions of each species is given in chapter 5 of this thesis. These represent some of the most dominant species in these forests, and were present in all forests studied here. Three individuals of each species were selected per forest, taking into consideration aspects regarding general accessibility, tree size (DBH > 50cm, height > 12m < 28m), and understorey density (< 20%), and at a minimum distance of 15 m apart. As far as possible, these trees also represented a range of different soil depths (according to rockiness of the terrain), distances from surface water (annual streams), and competition from other trees (canopy densities). Therefore, 24 individual trees were selected per forest, with 15 individual trees per species across the five forests (120 tree individuals in total).

Selected trees were treated with a chemical insecticide fog for 2 min in the early morning or late afternoon hours (between 05:00 and 07:00 or after 18:00) and only during windless times, to avoid fog scatter and to ensure optimum height was obtained. Trees were fogged over the two summer months of January and February 2017, as these correspond to peak activity for arthropods in the region (Procheş & Cowling 2006). I used a Dyna-Fog IZ150TM fogging machine fogging machine (42 litres per hour solution output) and a pyrethroid insecticide blend (1% deltamethrin, 0.6% permethrin, 6% piperonyl butoxide, 5% aromatic hydrocarbon solvent and 88% diesel), obtained as ready-mix from Dyna-Fog Africa. This machine provided a strong, consistent cloud of fog that rose in the cool ambient forest conditions, due to its warm temperature. The fog was emitted at ground level (Sørensen 2003) for 2 min to fully envelope the focal tree and avoid lateral movement into neighbouring trees. Selected trees had dense canopies and little understorey, with no visible epiphytes, flowers, or fruit, and had little overlap with neighbouring tree canopies. Where understorey was present, vegetation was either bent away from the immediate fogging area, or removed using a machete. Two collecting sheets, each 320 cm x 148 cm in size, equating to 9.47m², were placed underneath the crown of the focal tree, while avoiding areas that also contained branches of other trees. Sheets were suspended ca. 1 metre from the forest floor using steel stakes and rope to avoid litter fauna moving onto sheets. Collecting sheets remained under the focal trees for 50 min after insecticide application to ensure maximal collection time before larger arthropods started to recover. All arthropod samples on the collecting sheets were then transferred to collecting jars containing 70% ethanol.

Table 1: List of sampled tree species including their higher taxonomic classification

Order	Family	Host species
Oxidales	Cunoniaceae	*Cunonia capensis*
Cornales	Curtisiaceae	*Curtisia dentata*
Lamiales	Oleaceae	*Olea capensis macrocarpa*
Myrtales	Penaeaceae	*Olinia ventosa*
Pinales	Podocarpaceae	*Podocarpus latifolius*
Celastrales	Celastraceae	*Pterocelastrus tricuspidatus*
Oxidales	Cunoniaceae	*Platylophus trifoliatus*
Ericales	Myrsinaceae	*Rapanea melanophloeos*

Arthropods

Collected arthropods were sorted to morphospecies and identified to order. Where possible, they were identified to family level, with spiders and ants identified to genus and/or species level. To test the three hypotheses, all arthropods were additionally grouped according to their functional feeding guild using field guides and by examining their mouthparts (Labandeira 1997), specific to the life stage of the specimen collected (Scholtz & Holm 1985). Herbivorous arthropods included, among others, beetle families such as leaf beetles and weevils, bug families such as plant- and leafhoppers, lepidopteran larvae, orthopterans, and thrips. Detritivorous arthropods included cockroaches, numerous beetle families, amphipods, isopods, earwigs, barklice, and bristletails. As flies have high diversity in forest canopies (Basset 2001) and diverse feeding strategies, I treated these as a separate group. Similarly, all ant species, having a wide range of diets, were placed in a separate group. Predators comprised all spiders, pseudoscorpions, predatory wasps, parasitoids, beetle families such as ladybirds, ground beetles, and rove beetles, as well as hemipterans such as thread-legged bugs (Emesinae). A reference collection of all morphospecies are housed at the Entomology Museum, Stellenbosch University, but spiders housed at the South African National Collection of Arachnida, Pretoria, and all hymenopterans, including the ants, at Iziko Museum, Cape Town.

Plant characteristics

I collected random, intact and mature leaves from the lower branches of each individual focal tree using a pole pruner and, where necessary, a ladder. Leaves were air dried for 4 months in brown paper bags. After this time, 0.02 g powdered dry leaf material was sent to the Stable Isotope Laboratory at the Department of Archaeology, University of Cape Town, South Africa to determine total nitrogen content, total carbon content, carbon: nitrogen ratio, $\delta_{15}N/_{14}N$ isotope ratio and the $\delta_{13}C/_{12}C$ ratio for each individual tree. Around each focal tree, a circular plot was established with a radius of 11.3 m, equating to a plot size of *ca*. 400 m^2. In each plot, the DBH of the focal tree was measured, its height estimated by a single observer, and its percentage canopy cover estimated relative to the plot. If the focal tree covered the whole plot, a cover rating of 100% would be given. If the focal tree covered a quarter of the plot, a cover rating of 25% would be given (Fig. 2). For all other trees in the plot with a DBH larger than 15 cm, we determined the species identity and percentage canopy cover. Thus, due to canopy overlap, the total cover per plot could be more than 100%.

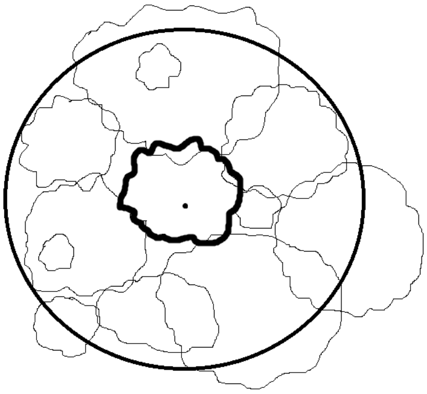

Figure 5: Circular plot surrounding focal tree, here with an estimated focal tree canopy cover (in bold) of ca. 15%.

Statistical analyses

Effect of tree identity and plot characteristics on canopy arthropod diversity (H1)

Species estimates were performed in PRIMER 6, using the Chao2 and Jacknife2 estimates (Clarke & Gorley 2006). Both abundance and species richness data for the respective guilds were tested for overdispersion in R. Overdispersed data were analysed using the negative binomial family, with equidispersed data analysed using the Poisson distribution family. Generalized linear mixed models were constructed for both abundance and species richness using the package *glmmTMB* in R (Brooks et al. 2017). This was done for each of the respective guilds, with each model containing the variables focal tree identity (species), focal tree canopy cover, host same-species canopy cover in plot, plot tree species richness, and plot canopy cover, with forest identity (re: patch) included as a random variable in the model. Pair-wise differences for abundance and species richness for which host identity revealed significance, were separated using a Tukey post-hoc test using the *emmeans* package in R (Magnusson et al. 2017).

To determine differences in arthropod assemblages between the selected tree species, I conducted permutational multivariate analysis of variance (PERMANOVA) in the programme PRIMER 6 (Clarke

& Gorley 2006). For this, data were square-root transformed, and assessed using Bray-Curtis similarity matrices. The respective effects of the multiple variables, as mentioned above, were included in the model using distance based linear modelling (DistLM) based off of Bray-Curtis similarity matrices, using specified selection. This method allows for the addition of variables to the analyses based on their total variation explained, until no further variables improve the model based on AICc (Burnham & Anderson 2004).

Effect of tree identity and plot characteristics on tree physiological features (H2)

Data for total content of foliar nitrogen and carbon were subjected to Yeo-Johnson transformation using the *bestNormalize* package in R version 3.5.1 (Peterson 2019) to normalise. Data for δ15N/14N, C/N and δ13C/12C had normal distributions, determined through Shapiro-Wilks W statistics, and were not transformed. Linear mixed-effect modelling (LMMs) were constructed to evaluate the effect of the various plot factors on these data, using the *lme4* package in R (Bates *et al*. 2007). Each model contained the variables focal tree identity (species), focal tree canopy cover, host species canopy cover, plot tree species richness, and plot canopy cover, with forest identity included as a random variable in the model (Bolker *et al.* 2009). Pair-wise differences for the variables for which host identity had a significant influence, were again separated again using a Tukey post-hoc test.

Effect of within-host physiological features on arthropod diversity (H3)

To test to what extent tree physiological features explained variation in arthropod species richness and abundance for each of the arthropod groups, several candidate models were evaluated for each tree species separately. The full model included the variables N, C, δ15N/14N, C/N and δ13C/12C, with forest identity included as random variable, and the response variable was either abundance or species richness for each of the arthropod guilds. The candidate models for each guild totalled 32, with each model containing a unique combination of variables. Relative support for the models was then assessed using the AICc criterion with best model selection using the package *AICcmodavg* in R, after which

Generalised Linear Mixed Models (GLMMs) were computed using the candidate model with the lowest AICc.

To explain variation in arthropod assemblage composition as described by the five plant characteristics, distance-based linear modelling (DistLM) was performed for each arthropod guild, on each tree species, based on Bray-Curtis similarity matrices, using specified selection in PRIMER 6 (Clarke & Gorley 2006).

Results

In total, 20 734 arthropod individuals were collected during the study, comprising 1 538 species. Estimates of species richness of 2 636.1 (± 113.0) and 2 737.8 were obtained for Chao2 and Jacknife2 estimates respectively, indicating that I sampled just more than 56% of estimated species richness. A more detailed summary of the arthropod taxonomic diversity sampled is given in chapter 5 of this thesis.

Predators were the most species-rich guild, totalling 732 species and comprising 47.6% of all sampled species (Fig. 3). They was followed by herbivores, with 369 species, flies (211 spp.), detritivores (106 spp.), and ants (36 spp.). Predators were also the most abundant guild, with 7 621 individuals, comprising 36.8% of all sampled individuals. 1 175 (5.67% of all catches) were ants. The herbivores contained 6 064 individuals, 29.3% of all catches.

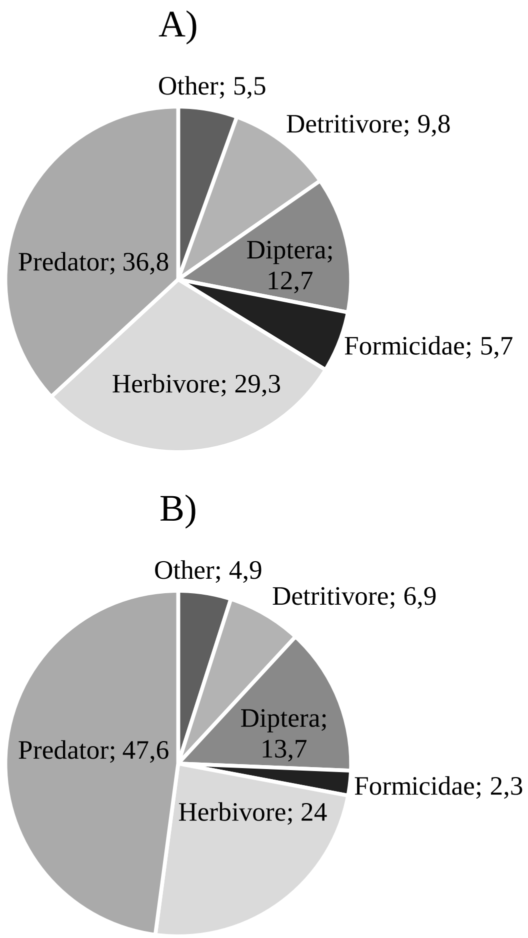

Figure 3: Percentage contribution of the guilds including 'Other' (fungivores, pollinators) relative to each other, expressed both as abundance (A) and species richness (B) for canopy sampled arthropods across all tree species.

Effect of tree identity and plot characteristics on canopy arthropod diversity (H1)

Arthropod species richness varied between a mean of 49.2 (± 5.13) and 80.07 (± 8.87), and abundance varied between 125.93 (± 23.86) and 213.2 (± 29.71) between the different tree species (Table 2). Focal tree identity was an important explanatory variable for differences in arthropod abundance for overall arthropods, herbivores, and flies (Table 3). However, no significant differences between particular tree species were found after post-hoc analyses for the overall arthropods collected or the herbivores. Dipterans were most abundant in the canopy of *C. dentata* and least abundant in the canopies of *P.*

tricuspidatus, but abundance was similar between all other species (Supplementary material, fig. S1). Plot canopy cover was the second most important factor explaining the abundance of collected arthropods. Contrary to expectations, plot cover was negatively correlated to abundance of overall arthropods, herbivores, predators, and detritivores (Table 3). However, detritivores were more abundant in focal trees with high canopy cover. Ant abundance was only affected by tree species richness, and to which it was negatively correlated (Table 3).

Similar to arthropod abundance, arthropod species richness for overall arthropods, herbivores, predators and flies, were significantly influenced by focal tree identity (Table 3). Highest overall species richness was in canopies of *C. dentata*, followed by *P. latifolius* (Supplementary material, fig. S2). Lowest species richness was in canopies of *P. trifoliatus*. Also, *C. dentata* hosted significantly more herbivore species in its canopies than *P. trifoliatus* and *R. melanophloeos* (Supplementary material, fig. S3). Similar patterns were present for predators and detritivores (Supplementary material, figs. S4-S5), with the flies being least species rich in canopies of *P. tricuspidatus* (Supplementary material, fig. S6). Species richness of all guilds was negatively correlated to total plot canopy cover, except for ants, which were not affected by any of the variables included here. Unexpectedly, species richness for overall arthropods collected, predators, and detritivores was negatively correlated with focal tree cover. Increased cover of host tree species in a plot led to a decrease in overall arthropod richness collected, and in richness of predators. An increase in tree species per plot led to an increase in species richness of predatory arthropods.

Table 2: Summary statistics of mean abundance and species richness (± SE) sampled per individual tree from each of the respective tree species (n = 15) for the respective canopy arthropod guilds.

Diversity indices	*C. capensis*	*C. dentata*	*O. c. macrocarpa*	*O. ventosa*	*P. trifoliatus*	*P. latifolius*	*P. tricuspidatus*	*R. melanophloeos*
Abundance	188.73 ± 29.1	213.2 ± 29.71	171.2 ± 15.02	204.13 ± 28.89	125.93 ± 23.86	188.8 ± 26.47	147 ± 25.57	143.27 ± 24.32
Spp. richness	67.4 ± 7.7	80.07 ± 8.87	65.47 ± 4.28	69.73 ± 7.7	49.2 ± 5.13	66.67 ± 4.92	59.53 ± 6.97	62.87 ± 8.02
Herbivore abund.	50.4 ± 8.66	62 ± 11.49	58.27 ± 7.35	63.07 ± 12.48	36.27 ± 10.35	62.2 ± 13.12	39.33 ± 7.33	36.6 ± 6.07
Herbivore spp. r.	15.27 ± 1.76	18.4 ± 2.6	16.13 ± 1.38	15.8 ± 2.06	11 ± 1.06	16.27 ± 1.33	15 ± 2	13.07 ± 1.32
Predator abund.	68.2 ± 13.45	83.27 ± 12.11	58.33 ± 6.49	81.27 ± 13.72	43.07 ± 8.62	65.8 ± 8.12	55.73 ± 11.57	52.07 ± 11.48
Predator spp. r.	29.93 ± 4.14	38.4 ± 4.95	30.4 ± 2.91	34.93 ± 4.62	20.67 ± 2.96	31.13 ± 2.78	27.33 ± 4.19	29.73 ± 4.64
Detritivore abund.	20.6 ± 3.34	16.6 ± 3.13	16.27 ± 3.9	18.93 ± 4.07	12.8 ± 2.6	22.27 ± 5.04	12.8 ± 2.03	15.13 ± 3.06
Detritivore spp. r.	7.13 ± 0.79	7.2 ± 0.9	5.73 ± 0.76	6.07 ± 0.76	4.6 ± 0.58	6 ± 0.59	6.13 ± 0.75	6.73 ± 1
Fly abund.	31.13 ± 9.53	27.53 ± 4.55	21.4 ± 3.55	15.2 ± 1.62	25.2 ± 6.77	22.67 ± 4.61	13.4 ± 1.99	19.6 ± 3.7
Fly spp. r.	9.07 ± 1.29	10.47 ± 1.36	7.27 ± 0.84	7.67 ± 0.76	9.13 ± 1.35	8 ± 1.59	6 ± 0.58	7.6 ± 1.04
Ant abund.	8.73 ± 2.41	10.53 ± 3.29	6.87 ± 1.63	16.13 ± 5.13	4.53 ± 1	7.87 ± 4.33	15.73 ± 6.31	8.13 ± 4.89
Ant spp. r.	2.47 ± 0.36	1.53 ± 0.24	2.07 ± 0.33	2.73 ± 0.44	1.67 ± 0.33	1.93 ± 0.36	2.73 ± 0.57	1.47 ± 0.34

Table 3: Results of the Generalized linear mixed modelling indicating the estimates of each of the model variables for the respective arthropod guilds for abundance and species richness data.

		Abundance		Species richness	
Guild	Variable	Estimate	Chi-square	Estimate	Chi-square
Overall	Focal tree identity	5.51 ± 0.24	**14.55***	4.35 ± 0.07	**158.22*****
	Focal tree cover	5.67 ± 0.26	1.32	4.45 ± 0.07	**21.49*****
	Host species cover	5.64 ± 0.26	0.53	4.43 ± 0.07	**11.59*****
	Plot richness	5.76 ± 0.21	1.08	4.48 ± 0.06	**9.47****
	Plot cover	5.52 ± 0.27	**12.10*****	4.26 ± 0.08	**101.88*****
Herbivore	Focal tree identity	4.57 ± 0.32	**15.99***	3.12 ± 0.12	**43.87*****
	Focal tree cover	4.63 ± 0.34	0.25	3.17 ± 0.13	1.79
	Host species cover	4.71 ± 0.34	1.55	3.18 ± 0.13	2.17
	Plot richness	4.60 ± 0.28	0.02	3.11 ± 0.11	0.02
	Plot cover	4.53 ± 0.37	**10.82****	3.01 ± 0.14	**26.23*****
Predator	Focal tree identity	4.48 ± 0.27	13.16	3.45 ± 0.10	**114.33*****
	Focal tree cover	4.61 ± 0.29	1.49	3.52 ± 0.11	**17.95*****
	Host species cover	4.50 ± 0.29	0.01	3.46 ± 0.11	**5.06***
	Plot richness	4.63 ± 0.24	0.47	3.60 ± 0.10	**13.14*****
	Plot cover	4.43 ± 0.30	**6.01***	3.29 ± 0.12	**48.80*****
Detritivore	Focal tree identity	2.62 ± 0.34	11.98	2.13 ± 0.19	**15.15***
	Focal tree cover	3.03 ± 0.37	**7.12****	2.35 ± 0.21	**3.92***
	Host species cover	2.87 ± 0.36	0.23	2.28 ± 0.21	0.64
	Plot richness	3.20 ± 0.32	3.13	2.12 ± 0.19	0.90
	Plot cover	2.72 ± 0.38	**8.46****	2.16 ± 0.23	**6.43***
Flies	Focal tree identity	3.63 ± 0.31	**18.51****	2.35 ± 0.16	**30.20*****
	Focal tree cover	3.91 ± 0.32	0.11	2.48 ± 0.18	0.14
	Host species cover	3.91 ± 0.32	0.15	2.55 ± 0.18	1.01
	Plot richness	3.87 ± 0.28	0.17	2.67 ± 0.15	2.58
	Plot cover	3.88 ± 0.33	2.83	2.43 ± 0.18	**12.73*****
Ants	Focal tree identity	1.37 ± 0.59	13.34	0.40 ± 0.33	12.83
	Focal tree cover	1.10 ± 0.68	0.05	0.59 ± 0.38	3.82
	Host species cover	1.34 ± 0.66	1.33	0.54 ± 0.37	2.29
	Plot richness	2.09 ± 0.63	**7.29****	0.66 ± 0.32	1.36
	Plot cover	0.97 ± 0.69	0.90	0.32 ± 0.38	2.01

* $P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Similar to the other arthropod diversity measures, arthropod assemblage composition was significantly affected by focal tree species identity (Table 4). The tree species with the most dissimilar overall assemblages was *C. dentata* (similar only to *P. latifolius*), *O. c. macrocarpa* (similar only to *C. capensis*) and *O. ventosa* (similar only to *P. latifolius*). Herbivores were most dissimilar in *O. c. macrocarpa* and *P. trifoliatus* in terms of their assemblages, with *R. melanophloeos* hosting the most generalist herbivore assemblages. Predator and fly assemblages were most dissimilar in canopies of *C. dentata*, and detritivore assemblages in canopies of *P. trifoliatus*. Ant assemblages were unaffected by host tree species. Focal tree canopy cover affected only detritivore and ant assemblages. Total cover of host tree species within a plot significantly affected overall, herbivore, and predator assemblages (Table 5). Tree species richness affected only the herbivore assemblages. Assemblages of all arthropod guilds together were significantly affected by total plot canopy cover.

Table 4: Results of the Permutational Multivariate Analysis of Variance indicating similarities in arthropod assemblages between selected tree species for each respective arthropod guild. Reported t-values for pairwise differences. Significance indicated in bold.

Guild	Pseudo-F	Host species	*C. capensis*	*C. dentata*	*O. c. macrocarpa*	*O. ventosa*	*P. latifolius*	*P. tricuspidatus*	*P. trifoliatus*
Overall	**1.86*****	*C. capensis*	x						
		C. dentata	**1.21***	x					
		O. c. macrocarpa	1.01	**1.26****	x				
		O. ventosa	**1.21***	**1.28****	**1.28****	x			
		P. latifolius	1.16	1.15	**1.19***	1.02	x		
		P. tricuspidatus	**1.26***	**1.21***	**1.34****	**1.27***	**1.19***	x	
		P. trifoliatus	1.14	**1.40*****	**1.22***	**1.36****	**1.19***	**1.33****	x
		R. melanophloeos	1.11	**1.22***	**1.21***	**1.21***	1.11	1.00	1.13
Herbivores	**2.05*****	*C. capensis*	x						
		C. dentata	**1.33***	x					
		O. c. macrocarpa	0.79	**1.32***	x				
		O. ventosa	**1.37***	1.18	1.18	x			
		P. latifolius	1.14	1.22	**1.26***	1.20	x		
		P. tricuspidatus	**1.43****	1.08	**1.46****	0.88	1.17	x	
		P. trifoliatus	1.19	**1.30***	**1.25***	**1.25****	**1.38***	1.17	x
		R. melanophloeos	0.95	1.25	1.25	1.25	**1.40****	0.96	0.86
Predators	**1.62*****	*C. capensis*	x						
		C. dentata	1.09	x					
		O. c. macrocarpa	0.98	**1.31****	x				
		O. ventosa	1.11	**1.25****	**1.33****	x			
		P. latifolius	1.14	**1.19***	1.09	1.00	x		
		P. tricuspidatus	**1.30****	**1.19***	**1.22***	1.07	1.05	x	
		P. trifoliatus	**1.21***	**1.35****	**1.24***	**1.32****	1.17	0.99	x
		R. melanophloeos	**1.21***	**1.23***	1.13	1.01	1.04	0.97	1.05
Detritivores	**2.19*****	*C. capensis*	x						
		C. dentata	1.30	x					
		O. c. macrocarpa	0.75	0.73	x				

		O. ventosa	1.32	0.95	0.95	x			
		P. latifolius	0.94	1.02	1.06	0.94	x		
		P. tricuspidatus	**1.42***	1.33	**1.44***	1.03	1.32	x	
		P. trifoliatus	**1.32***	**1.75****	**1.79*****	**1.89*****	**1.72*****	**1.72*****	x
		R. melanophloeos	0.57	0.44	1.19	1.17	1.05	**1.50***	1.19
Flies	**1.87*****	*C. capensis*	x						
		C. dentata	**1.38***	x					
		O. c. macrocarpa	1.30	1.27	x				
		O. ventosa	1.08	**1.43****	1.21	x			
		P. latifolius	1.32	**1.38***	1.03	1.11	x		
		P. tricuspidatus	**1.37***	**1.40***	**1.43***	1.07	1.03	x	
		P. trifoliatus	**1.30***	**1.37***	1.30	1.22	1.05	1.19	x
		R. melanophloeos	1.14	**1.41***	1.13	1.04	1.19	1.18	**1.36***
Ants	0.97								

* $P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Table 5: Results of the distance-based linear modelling indicating the significance of the selected variables on assemblages of different arthropod guilds from the canopies, regardless of species.

Variable	Statistic	Overall	Herbivores	Predators	Detritivores	Flies	Ants
Focal tree cover	AICc	972.97	965.45	973.84	949.38	973.32	931.17
	SS	4148.10	4465.30	3071.60	5101.90	2689.30	6094.90
	Pseudo-F	1.27	1.46	0.93	**1.90***	1.11	**2.65****
	Prop. Variance	0.01	0.01	0.01	0.02	0.01	0.02
	Cum. Variance	0.01	0.01	0.01	0.02	0.01	0.02
Host same-species cover	AICc	973.37	965.62	974.37	950.15	938.47	931.29
	SS	5417.30	5797.70	5066.20	3508.50	2257.80	4456.70
	Pseudo-F	**1.67****	**1.91****	**1.55****	1.31	0.93	1.95
	Prop. Variance	0.01	0.02	0.01	0.01	0.01	0.02
	Cum. Variance	0.03	0.03	0.02	0.03	0.02	0.04
Plot richness	AICc	974.36	965.96	975.56	951.23	939.86	932.44
	SS	3646.80	5302.70	3023.30	2755.00	1781.90	2203.30
	Pseudo-F	1.13	**1.75***	0.92	1.03	0.73	0.97
	Prop. Variance	0.01	0.02	0.01	0.01	0.01	0.01
	Cum. Variance	0.03	0.04	0.03	0.04	0.02	0.05
Plot cover	AICc	974.61	966.36	976.13	951.53	939.30	932.60
	SS	5980.20	5147.80	5049.60	4823.20	6358.70	4407.70
	Pseudo-F	**1.86*****	**1.71***	**1.55****	**1.82****	**2.65*****	**1.94***
	Prop. Variance	0.02	0.01	0.01	0.02	0.02	0.01
	Cum. Variance	0.05	0.06	0.04	0.05	0.05	0.06

* P < 0.05, **P < 0.01, ***P < 0.001.

Effect of tree identity and plot characteristics on tree physiological features (H2)

Except for foliar C, which was negatively correlated to plot cover (Fig. 4), all plant physiological features were influenced only by tree identity (Table 6). Foliar N was significantly higher in *O. ventosa* (Supplementary material, fig. S7). Large variance around means were found for δ15N/14N between tree species (Supplementary material, fig. S8). Significantly higher leaf C occurred in the case of *C. dentata* compared to all other tree species (Supplementary material, fig. S9), with *C. capensis* having the lowest levels of foliar C. Three tree species, *C. capensis*, *O. ventosa* and *P. latifolius*, had significantly higher levels of foliar δ13C/12C compared to *O. c. macrocarpa*, *P. tricuspidatus*, *P. trifoliatus* and *R. melanophloeos* (Supplementary material, fig. S10). The remaining species, *C. dentata*, showed intermediate levels of δ13C/12C. Inverse to foliar N, *O. ventosa* showed the lowest C/N ratio (Supplementary material, fig. S11).

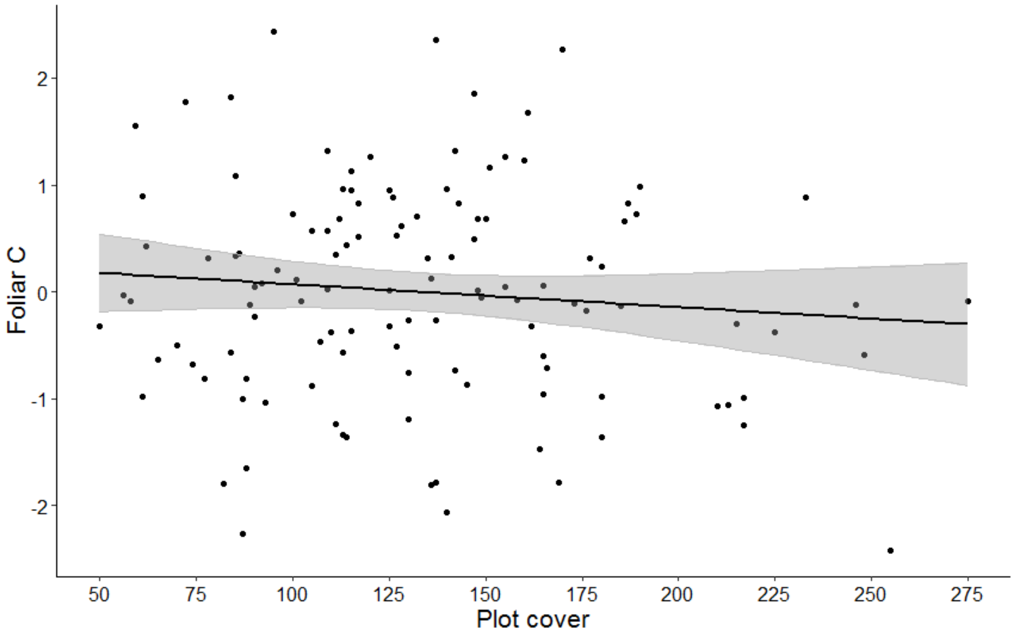

Figure 4: Scatterplot of foliar C in response to plot cover for all tree species studied, with a best-fit line and 95% confidence levels.

Table 6: Results of the linear mixed models indicating the estimates of each of the model variables for the respective plant physiological variables. Significance indicated in bold.

Physiological variable	Variable	Estimate	Chi-square
Nitrogen	Focal tree identity	-0.08 ± 0.42	**97.49*****
	Focal tree cover	-0.92 ± 0.33	1.68
	Host species cover	-1.02 ± 0.34	0.14
	Plot richness	-0.89 ± 0.27	0.55
	Plot cover	-1.09 ± 0.35	1.47
δ15N/14N	Focal tree identity	-0.84 ± 0.85	**43.43*****
	Focal tree cover	-2.36 ± 0.84	2.10
	Host species cover	-2.58 ± 0.83	0.34
	Plot richness	-2.86 ± 0.79	0.76
	Plot cover	-2.45 ± 0.86	2.49
Carbon	Focal tree identity	0.23 ± 0.44	**138.73*****
	Focal tree cover	-1.12 ± 0.31	0.02
	Host species cover	-1.10 ± 0.31	0.06
	Plot richness	-0.87 ± 0.27	2.31
	Plot cover	-1.22 ± 0.32	**5.72***
δ13C/12C	Focal tree identity	-30.12 ± 0.57	**66.06*****
	Focal tree cover	-28.82 ± 0.52	2.00
	Host species cover	-28.96 ± 0.52	0.37
	Plot richness	-29.24 ± 0.42	0.45
	Plot cover	-29.12 ± 0.54	2.42
C/N	Focal tree identity	40.63 ± 3.75	**112.58*****
	Focal tree cover	46.35 ± 2.84	0.89
	Host species cover	46.98 ± 2.87	0.03
	Plot richness	44.92 ± 2.36	1.59
	Plot cover	47.57 ± 2.93	1.55

* P < 0.05, **P < 0.01, ***P < 0.001.

Effect of within-host physiological features on arthropod diversity (H3)

Arthropod abundance varied considerably in response to within-species variation of all measured plant physiological features (Table 7). Overall arthropod abundance was significantly positively correlated to foliar N, while negatively correlated to foliar C for *C. capensis*. The converse was the case for association between overall arthropods collected from *P. tricuspidatus* and *P. trifoliatus* canopies, in which overall arthropod abundances negatively correlated with foliar N, and positively to foliar C. Similarly, among herbivores, abundance revealed positive correlations to foliar N and negative correlations to foliar C in some host species (*C. capensis*, *O. c macrocarpa* and *O. ventosa*), and a converse pattern in others (*P. tricuspidatus* and *P. trifoliatus*). Overall arthropod abundance significantly correlated with foliar δ13C/12C in all tree canopies. However, in certain host species these correlations were positive and in others negative. Herbivore abundances revealed significant correlations to foliar δ13C/12C and total C in all tree canopies, except *R. melanophloeos*. These responses ranged from being either positive or negative, depending on identity of the host species. Herbivore abundances showed little correlation towards foliar δ15N/14N, but predator and fly abundances significantly correlated to δ15N/14N in three host species. Ants were the guild most responsive to foliar δ15N/14N, with five tree species revealing correlations in ant abundances and δ15N/14N. However, these correlations were either positive or negative, again depending on the host species. Herbivores were especially responsive to the C/N ratio in leaves. Herbivore abundances correlated positively (*C. capensis*, *C. dentata*, *O. c. macrocarpa* and *O. ventosa*) and negatively (*P. tricuspidatus* and *P. trifoliatus*) to the C/N ratio. For two host species, herbivores were unaffected by changes in the C/N ratio.

Similar to arthropod abundance, species richness varied considerably in response to within-species variation of the measured plant physiological features (Table 8). Overall species richness both positively and negatively correlated with foliar N, depending on the host species identity. Herbivore species richness positively correlated with foliar N in only one host species, *P. latifolius*. From canopies of *P. latifolius*, fly richness also positively correlated with foliar N. Predators revealed mixed patterns in response to variation in foliar N. Richness responses mostly showed significantly negative correlations with leaf δ15N/14N. However, overall and predator richness positively correlated with leaf δ15N/14N in canopies of *P. tricuspidatus*. Overall species richness was negatively correlated with leaf C levels, in *C. capensis* and *P. trifoliatus* canopies. Herbivores too, showed negative responses to foliar C, but in *C. capensis* canopies only. When any given guild significantly correlated to foliar C, it was always negative. Overall species richness revealed a significantly positive relationship with δ13C/12C in canopies of *O. ventosa*, *P. trifoliatus* and *P. latifolius*, with a negative correlation occurring in canopies of *C. capensis* trees only. Herbivore richness positively correlated with δ13C/12C, but only in *O. ventosa* canopies. Predator richness positively correlated with δ13C/12C, but only in canopies of *O.*

ventosa, *P. trifoliatus* and *P. latifolius*. Richness responses showed no general patterns in relation to the C/N ratio of leaves, again with the identity of host species giving differential responses.

Table 7: Results of the model selection procedure (based on second order Akaike Information Criterion) indicating the correlations of measured plant characteristics on canopy arthropod abundances for each of the respective arthropod guilds between eight tree species. Reported z-values.

Guild	Variable	*C. capensis*	*C. dentata*	*O. capensis macrocarpa*	*O. ventosa*	*P. latifolius*	*P. tricuspidatus*	*P. trifoliatus*	*R. melanophloeos*
Overall	N	5.51***		-2.82**			-6.67***	-4.78***	
	δ15N/14N	2.94**	-3.58***	-2.84**			5.78***		-16.67***
	C	-8.07***	-4.73***		-5.69***	4.08***	5.01***	2.19*	
	δ13C/12C	-5.30***	2.71**	-4.41***	3.90***	11.02***	-5.62***	13.94***	3.45***
	C/N	5.21***		-6.04***	4.51***	-9.63***	-9.19***	-4.45***	
Herbivores	N	4.85***		4.46***	2.79**		-4.01***	-3.26**	
	δ15N/14N								-5.93***
	C	-6.83***	-4.61***	-5.13***	-4.92***	6.72***	8.07***	4.28***	
	δ13C/12C	-3.78***	10.11***	-3.24**	-5.04***	6.05***	-6.77***	8.15***	
	C/N	4.49***	6.22***	4.06***	3.98***		-5.15***	-3.20**	
Predators	N		2.33*				-7.61***		
	δ15N/14N						12.34***	-4.67***	-11.60***
	C	-6.36***	-6.02***	3.54***	-3.67***			-4.78***	
	δ13C/12C	-5.84***		-5.04***	8.12***	6.85***	-2.69**	6.70***	
	C/N	-3.77***				-7.62***	-8.89***		
Detritivores	N			-3.32***	6.09***	3.34***			
	δ15N/14N	-7.00***	-3.49***	-3.06**					-5.70***
	C			3.08**	-4.65***	-3.73***	2.23*		
	δ13C/12C	4.34***	-2.27*			2.45*		2.41*	
	C/N	-3.24**		-4.50***	6.39***		-2.54*		
Flies	N	6.15***		-4.16***		6.12***	-2.74**	-6.01***	
	δ15N/14N	6.94***	-3.12**						-5.51***
	C	-7.01***						-3.74***	
	δ13C/12C					7.96***		8.57***	-2.79**
	C/N	6.20***		-6.52***		5.40***	-3.00**		
Ants	N	-5.00***	2.01*			-6.07***			

δ15N/14N	2.45*		-3.43***	3.97***	-3.40***			-2.71**
C			-3.19**	-5.23***		7.83***		-1.97*
δ13C/12C	-2.88**	-4.79***		7.84***	3.00**	-7.99***		3.69***
C/N					-6.15***	-5.01***		

* $P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Table 8: Results of the model selection procedure (based on second order Akaike Information Criterion) indicating the effects of measured plant characteristics on canopy arthropod species richness for each of respective arthropod guilds between eight tree species. Reported z-values.

Guild	Variable	*C. capensis*	*C. dentata*	*O. capensis macrocarpa*	*O. ventosa*	*P. latifolius*	*P. tricuspidatus*	*P. trifoliatus*	*R. melanophloeos*
Overall	N	3.59***	-2.54*			4.58***	-4.47***		
	δ15N/14N		-4.20***				5.70***	-2.68**	-7.47***
	C	-6.01***						-3.13**	
	δ13C/12C	-2.39*			2.07*	5.08***		5.28***	
	C/N			-2.59**	3.93***		-4.88***		
Herbivores	N					2.18*			
	δ15N/14N								-2.73**
	C	-2.55*							
	δ13C/12C				2.11*				
Predators	N	2.21*					-3.44***	-2.23*	
	δ15N/14N		-2.87**				4.52***		-5.98***
	C	-5.67***							
	δ13C/12C				2.35*	3.62***		3.18**	
	C/N				2.68**	-2.74**	-4.00***		
Detritivores	δ15N/14N								-2.64**
	C	-2.07*				-2.02*			
	C/N				2.84**				
Flies	N					3.77***			
	δ15N/14N		-2.14*						-3.08**
	C							-2.61**	
	δ13C/12C	-2.15*				4.40***		2.82**	
	C/N				2.04*	3.47***			
Ants	δ15N/14N								-2.55*

* $P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

The most important variable explaining the variation in arthropod assemblages was δ15N/14N, with only one tree species, *C. dentata*, not revealing significance (Table 9). For four tree species, ant assemblages were best explained by the variable δ15N/14N. In *P. latifolius* canopies, herbivore assemblages were best explained by δ15N/14N. Changes in δ13C/12C led to changes in assemblages of overall, herbivore, detritivore and predators, although on only one host, *P. tricuspidatus* (Table 9). Different guilds responded differentially to plant physiological status, with responses specific to different tree species, with no general patterns being observed (Table 9).

Table 9: Results of the distance-based linear modelling (DistLM) sequential tests, indicating the most descriptive plant characteristics for each of the selected canopy arthropod guilds' assemblage composition between selected tree species.

Tree species	Guild	Variable	Pseudo-F	Variation explained (%)
C. dentata	NS	-	-	-
C. capensis	Ants	δ15N/14N	2.32*	14.96
	Predators	C	1.72*	10.75
O. ventosa	Overall	δ15N/14N	1.54*	7.81
	Flies	δ15N/14N	2.22**	13.86
	Ants	δ15N/14N	3.77**	22.24
O. c. macrocarpa	Ants	δ15N/14N	2.28*	15.30
	Predator	N	1.38*	9.61
P. latifolius	Herbivore	δ15N/14N	1.83*	12.03
P. tricuspidatus	Overall	δ15N/14N	1.57*	10.77
		δ13C/12C	2.16**	13.50
	Herbivore	δ13C/12C	1.89*	12.28
	Detritivore	δ13C/12C	2.26*	14.30
		C/N	1.94*	11.32
	Flies	N	2.27**	14.87
	Ants	δ15N/14N	2.63*	16.78
	Predators	δ13C/12C	1.96*	12.69
R. melanophloeos	Overall	δ15N/14N	1.64*	11.36
	Flies	δ15N/14N	2.67**	16.99
P. trifoliatus	Flies	δ15N/14N	1.87*	12.74

* $P < 0.05$, **$P < 0.01$, ***$P < 0.001$. NS = no significance.

Discussion

I provide a first account of the diversity and distribution of canopy arthropods in an African temperate rainforest complex. Canopies of these forests provide habitat for much diversity of species, with richness similar to that of northern temperate forests (Gering & Crist 2000), but considerably less than tropical regions (Allison et al. 1993) and other southern temperate rainforests studied to date (Arias et al. 2008). A full description of the taxonomic diversity, placed into a global context, forms part of chapter 5 of this thesis. As expected from other studies in this emerging field, tree species identity played a central role in dictating richness, abundance, and assemblage composition of canopy arthropods. Therefore, there seems to be limited movement of most arthropod taxa between the different tree species. With the exception of total plot cover, few plot-scale characteristics influenced arthropod diversity of focal trees. Except for foliar C concentration, plot characteristics also had little effect on plant physiological features. However, within-host variation in plant physiological features had significant effects on arthropod richness, abundance, and assemblage composition. Contrary to my expectations, arthropods on different hosts responded differently to variations in plant physiological features. For example, herbivore richness and abundance increased with decreased C isotope ratio on one species, but on another species, these showed a negative response. As the isotope ratio is a good indication of individual plant water stress (Walker et al. 2015a), these results show that there will likely be no uniformity in response of arthropod numbers towards increased drought periods as expected for the study region due to global climate change (Midgley et al. 2005).

Effect of tree identity on canopy arthropod diversity and tree physiological features

Host tree identity was an important factor dictating arthropod diversity sampled from tree canopies. This is in agreement with most global literature, with herbivorous arthropods being at least as specialized as pollinators (Forrest 2015; Hoiss et al. 2015; Ponisio et al. 2017; Jauker et al. 2019). This likely results from significant differences in tree morphology (Rivero-Lynch et al. 1996), physiology (Hunter & Lechowicz 1992), and phenology (Senn et al. 1992), with adaptations toward these becoming species-specific over evolutionary timescales (Darwin 1859). Here, differences in arthropod diversity between tree species were not only reflected by the herbivores, but also by other guilds, such as detritivores, predators and flies. Indeed, arthropod specialization towards different tree species do not seem to be restricted only to folivores (Wardaugh et al. 2013), and often shifts beyond lower trophic levels to include predatory arthropods (Esquivel-Gómez et al. 2017). Host preference is also evident in other kingdoms such as the fungi (Unterseher et al. 2007), which may explain responses of trophic groups such as the fungivores to host tree identity. Subsequently, many arthropod guilds can be considered host specific, albeit secondarily, and loss of even a single tree species from a forest system could result in substantial local extinctions (Régnier et al. 2009).

Here I showed that different tree species differ in many plant physiological variables, similar to a French Guianan rainforest (Hättenschwiler et al. 2008). This is partly due to different plant species showing different patterns in physiological investment during their life cycle, in a complex balancing attempt between available resources, reproduction, and defence (McGroddy et al. 2004). This can have a profound influence on arthropod diversity (War et al. 2018). For example, McGroddy et al. (2004), revealed that differences in N between trees could greatly affect eventual ecosystem processes, especially nutrient cycling, due to N investment in metabolic compounds. As such, N concentration is often an indication of leaf quality for insect herbivores, with foliar N variability affecting herbivore diversity and distribution, including herbivore feeding behaviour (Hosseini et al. 2018). Here, *O. ventosa* revealed the highest foliar N concentration, while also having the highest mean herbivore abundance per individual tree, which positively correlated with foliar N. However, the physiological variables measured here had differential impacts on arthropods, exhibiting stronger correlations within certain species, compared to relatively low or no impacts in other tree species. As such, not only a tree's visibly unique traits (i.e. phenology, morphology), but also its physiological differences compared to other species, appears to drive host preference in higher trophic levels.

Effect of plot characteristics on arthropod diversity and tree physiological features

Contrary to expectations based on resource concentration hypotheses (Hamback & Englund 2005; Wardhaugh 2014), and increases in microhabitats with denser foliage (Dial et al. 2006), I found a strong negative correlation between plot cover and arthropod diversity. This is similar to results of a study in Finland, where galling insect numbers on spruce trees decreased with increased cover (Muiruri et al. 2019). Decreased arthropod numbers due to increased canopy cover could be considered to be strongly linked to decreased light exposure of focal trees. For example, increased light availability may promote herbivores due to increased plant nutritional value (N-based) and decreased allocations towards plant defence compounds (C-based) (Roberts & Paul 2006). However, my data indicated that plant physiological features were unaffected by plot cover, with the exception of foliar C, which increased with lower plot cover around focal trees. This is similar to the results of Nichols-Orians (1991), where tannin concentration in leaves were greatest where light exposure was highest. Furthermore, canopy trees contain higher concentrations of phenols in sun-exposed leaves versus shade-leaves (Chandler & Goosem 1982; Waterman et al. 1984; Mole et al. 1988). Interestingly, here the foliar C increase correlated with higher arthropod diversity in more exposed focal trees, contrary to what would be expected, with light-exposed leaves having been shown to be less digestible and lower in quality for herbivores (Waterman et al. 1984). In line with the findings reported in the current study, however, Chacón & Arnesto (2006) reported increased carbon-based defences and greater herbivore damage among tree seedlings in temperate Chilean rainforest tree-fall gaps compared to forest interiors. Therefore, despite increases in carbon-based defences in more light exposed plants, herbivore numbers do not necessarily respond accordingly (Chacón & Arnesto 2006).

At the plot scale, arthropod diversity and distribution appears to be strongly driven rather by canopy structural variation, through the creation of numerous microhabitats, than by physiological variation per se. For instance, light exposure leads to increased temperatures that have positive effects on the development of arthropods. Leaf beetles, for example, perform better in open habitats where increased temperature and temperature variability, improves larval development (Sipura & Tahvanainen 2000). Although not explicitly tested here, the importance of light availability may therefore be a more important consideration for increased arthropod biodiversity than a subtle increase in available niches, as other research suggests. A canopy fogging study by Dial et al. (2006) reported greater numbers of arthropods where foliage was most dense. Indeed, increased canopy cover usually leads to increased structural complexity of the crown layer, which in turn can promote arthropod diversity by increased numbers of microhabitats (Grove 2002; Maeto et al. 2002; Campos et al. 2006; Jeffries et al. 2006), although my results do not support such a hypothesis.

Regardless of the exact mechanisms, i.e. light variation or structural variation, tree crown heterogeneity in mixed, diverse forests evidently affects arthropod diversity. The crown layer in many natural, mixed-species forests is characterized by great heterogeneity (Wolda 1983). Such a structurally complex layer might therefore promote arthropod diversity by providing microhabitats (re: tree crowns) ranging from highly exposed to light, i.e. forest gaps, to completely shaded, i.e. old growth stands, allowing for complementary arthropod diversity. This is supported by my results, with arthropod assemblage compositions also being significantly impacted by plot cover across different guilds. Therefore, similar to variations in tree species diversity, variations in plot cover promotes arthropod diversity. As found in Australia, biotic homogenization in plantation forests (species richness and cover) reduces ground-dwelling beetle diversity (Sweany et al. 2015), with yet untested impacts on canopy arthropods. This is concerning, as plantation forests are increasing worldwide (Nahuelhual et al. 2012), with large-scale homogenization occurring (Jongman 2002; Schulte et al. 2007; Hanberry et al. 2012). Moreover, the effects of climate change on natural forest succession, which would selectively affect the growth of co-occurring tree species (Andreu et al. 2007; Friedrichs et al. 2009), could increase risks of trophic cascades in canopy arthropod communities (Knight et al. 2005). However, these changes would be extremely difficult to monitor.

Effect of within-host physiological variation on arthropod diversity – implications for human induced environmental change

Resource availability and the balance of foliar chemistry in primary plant producers, and the subsequent effects on higher trophic levels, is a widely studied topic, but still poorly understood (Elser et al. 2000). Here, we reveal great effects of intra-specific variability in physiology on arthropod responses. This can be due to genetics (Nelson & Johnsen 2008; Hamanishi et al. 2010), but also often linked to differences in the availability of resources and individual plant stress levels (Arndt et al. 2001), i.e. moisture deficiencies (Schrader et al. 2005), or nutrient availability (Tuomi et al. 1984). Importantly, individual tree responses to stress may be greatly affected by climatic shifts (Lloyd et al. 2008). Over large biogeographical ranges, with great variation in local conditions, individuals of a single species may therefore experience different environmental stressors, which could lead to differential arthropod responses at the individual tree level. Individual trees under greater moisture stress (i.e. further from forest streams, nearer to edges, or occurring at the species' range extremities) might for example be more susceptible (Cobb et al. 1997) or less susceptible (Huberty & Denno 2004) to herbivory damage.

Viewing the stable isotope ratio of δ13C/12C as an indication of drought stress (Walker et al. 2015a), my results indicate that only certain species within mixed, diverse forests might show effects of drought stress on arthropod diversity. If droughts would occur over longer time periods, physiological variability within a single species might trigger complex responses, difficult to predict (Johnson et al. 2010). This is especially relevant in small, isolated forest patches with limited dispersal of many arthropod taxa between forest patches. For many arthropod species, being host-recurrent, shifting from one host species to another during stressful conditions will not be possible, and range shifts are strongly dependent on host adaptability (Hellmann et al. 2012). Subsequent ecological impacts of drought, or any shift in climatic regimes, could cause arthropod populations to undergo severe changes, threatening ecological integrity (Anderegg et al. 2015). Certain populations, arguably more generalist in nature, might be better able to move between host species, and become more numerous (Ward & Masters 2007; Roberts et al. 2011). However, host-specific responses of different arthropod guilds toward plant physiology, make predictions on how future climates might be shaping canopy communities especially difficult.

Here, most tree species showed some correlation between its physiology and associated arthropod diversity. Whereas terrestrial plants invest N mostly in metabolic compounds, C is more commonly used in structural and defensive compounds (McGroddy et al. 2004). The interaction between carbon-based physiology and arthropods in tree canopies becomes important to understand, especially under predictions of elevated levels of CO_2 globally (Walker et al. 2015b). It is possible that increases in CO_2 in the atmosphere will promote plant productivity, without similar increases in nutrient uptake (Dury et al. 1998), affecting the C/N ratio. Indeed, in exposing various *Quercus*-species to elevated levels of CO_2, has lead not only to a rise in foliar C/N ratios, but also to a decrease in associated insect herbivory (Hall et al. 2005), suggesting increased plant fitness. It has also been suggested that insect herbivores will have reduced fitness under elevated levels of CO_2 (Cornelissen 2011), through reduced growth rates and longer development time (Smith & Jones 1998; Goverde & Erhardt 2003), and reductions in food conversion efficiency (Lawler et al. 1996; Brooks & Whittaker 1998). Such changes would have substantial effects on higher trophic levels dependent on herbivores, such as insect predators. Alternatively, studies have shown how elevated CO_2 levels increases plant damage by aphids under modified conditions (Flynn et al. 2006). Predictably then, tree species will respond differentially towards elevated CO_2 levels, as they do to drought (Anderegg & Hillerislambers 2016) and pollution (Alahabadi et al. 2017), causing a wide array of stress on existing plant-insect interactions (Jactel et al. 2019).

Here, the C/N ratio revealed correlations with arthropod abundances and species richness across tree species, which varied between positive, neutral, and negative. The species in which C/N positively correlated with herbivore abundances (*C. capensis*, *C. dentata*, *O. c. macrocarpa* and *O. ventosa*), showed patterns opposite to what would be expected, given the general indicative use of C/N, again revealing the unpredictability of arthropod responses towards underlying tree physiology. The C/N ratio is important as indication of both food quality (-‘ve) and plant defences (+’ve) (Bazzaz et al. 1987; Gange & West 1994). However, increase in C/N causes increase in herbivore consumption, to compensate for diluted nitrogen concentrations in leaves (Coviella & Trumble 2000; Hunter 2001). In short, under elevated levels of C/N, herbivores have to eat more, and so spend more time feeding. This would necessarily increase the impact of herbivory on certain trees, and subsequent tree physiological responses. More compensating strategies by insect herbivores during increases in C/N include increased nitrogen utilization efficiency (Williams et al. 1994) and stimulation of enzymes detoxifying secondary metabolites in leaves (Lindroth et al. 1993). This means that increased C/N ratios would not necessarily guarantee decreased herbivore performance, as shown here and elsewhere (re: Awmack et al. 1997; Bezemer & Jones 1998).

Apart from drought and climate change, increases in temperature and pollution stemming from anthropogenic activities could also affect tree physiology (Wolfenden et al. 1990; Black et al. 2000; Stewart et al. 2002; Jones et al. 2008). Ambient temperature increases are predicted to increase soil warming in forests, which stimulates carbon gains in plant tissues (Melillo et al. 2011), whereas pollution significantly affected northern taiga forest trees to increase carbon and decrease nitrogen concentrations in foliage (Manninen et al. 2015). Such tree responses will have only speculative effects on associated arthropod biota. Here, the species with the highest foliar C levels, for example, showed a significantly negative correlation between foliar C and herbivore abundance. Predictably, increases in temperature, or pollution, will decrease fitness of herbivores associated with this species, which might see increased plant productivity partly through better C-based investment towards anti-herbivory defences. Other tree species which revealed positive associations between foliar C and herbivore diversity (e.g. *P. latifolius*), might face increased leaf damage under elevated temperatures.

Moreover, temperature will also have direct effects on canopy arthropod diversity. Laboratory studies show how altered temperature variability reduce forest insect fitness (David et al. 2017), and might shorten generation times, increasing risks of outbreaks (Bentz et al. 2019; Jactel et al. 2019). Higher temperatures could further increase insect mortality (Mech et al. 2018). Alternatively, some insect species will be able to expand their ranges with warmer temperatures (Roques et al. 2015), and develop faster (Jamieson et al. 2017). Therefore, predicting how insects, specifically forest arthropods dependent on trees, might respond to environmental change is not a simple procedure (Jactel et al. 2019), with my results indicating that these responses encompass factors associated with tree identity, plot characteristics, and plant physiology, notwithstanding the direct impacts of such changes on insect phenology.

An important precautionary factor, as noted by Dial et al. (2006), is that many arthropod species occupying tree canopies will still remain under sampled in fogging events, due to drift, or entanglement in branches and leaves. No study to date has assessed such impediments in fogging studies, which will necessarily affect reported results. Based on the correlative nature of my results, I conclude that the interaction between indigenous forest trees and canopy arthropods is a complicated, and currently poorly understood, field in ecology. Responses reported here are of a general nature, and clear patterns are lacking, which confirms the complexity of how canopy arthropods perceive not only differences in tree species, but also trees' varying physiology. Different tree species host different arthropod diversity levels, and are affected by aspects such as surrounding canopy structure and its physiology. In high diversity forests, I show that loss of just one tree species, anthropogenic homogenization of the crown layer, and/or human-induced environmental change, could lead to great community level changes, inevitably through local extinctions in higher trophic levels, and the potential loss of key pieces in the tree crown layer, nearly impossible to predict. In the light of forests currently experiencing change on a global scale (Hansen et al. 2013), I propose that factors relating to tree responses to climate change should be incorporated into canopy arthropod studies. Since the 1970's, global temperatures have risen (Allen et al. 2010). With many forests now facing increases in the intensity and incidence of drought, directly impacting the lungs of the planet (Christensen et al. 2007; Seager et al. 2007), we need to commit more work to understanding these effects on the 'last biotic frontier'.

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Supplementary material

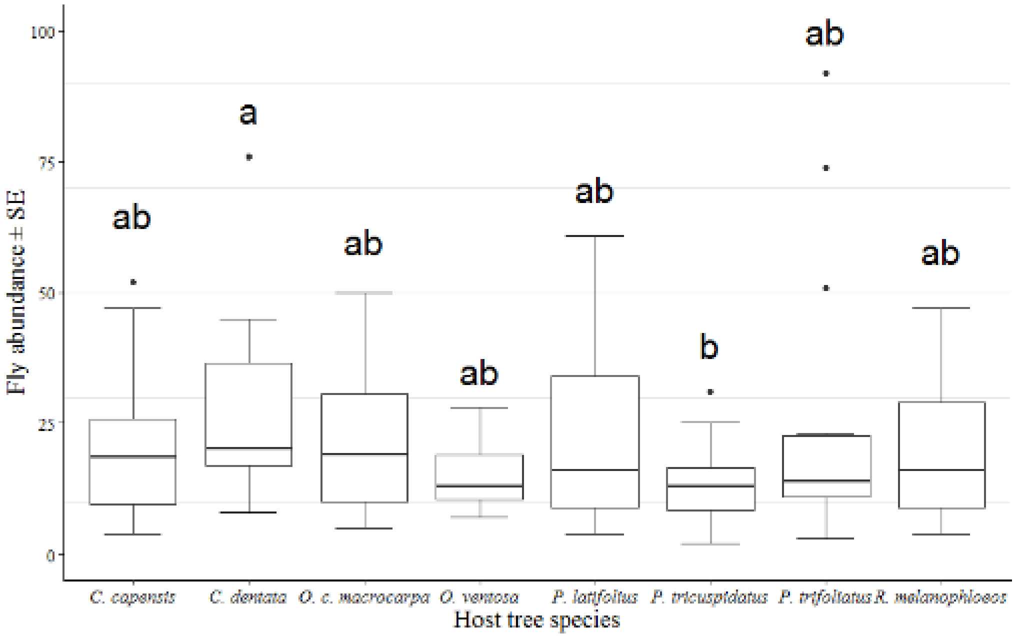

Figure S1: Box-and-whisker plots indicating between host differences in medians of fly abundances determined by GLMMs with shared letters above plots indicating similar medians

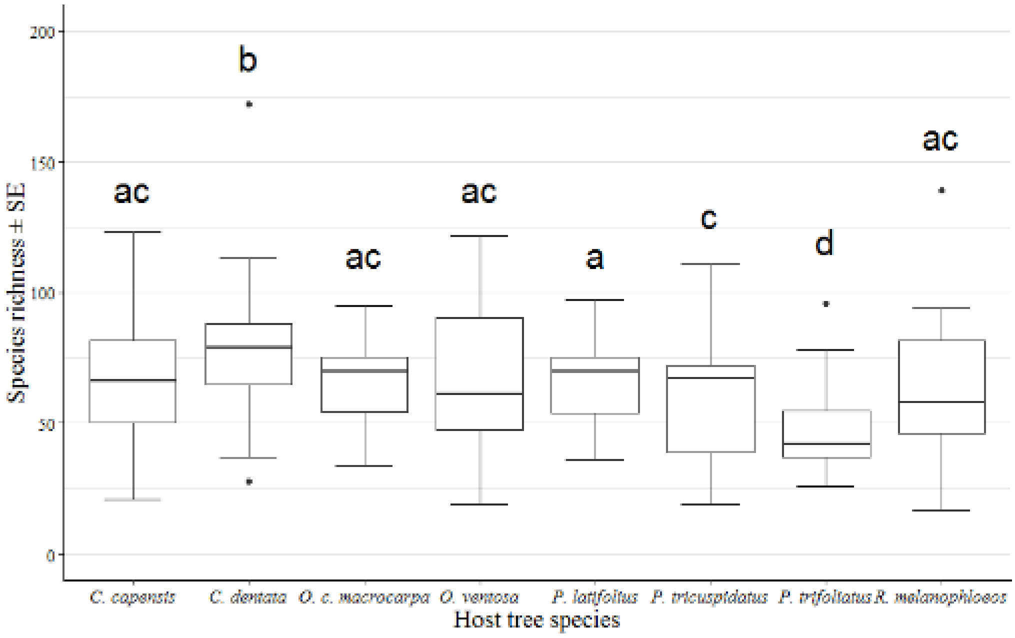

Figure S2: Box-and-whisker plots indicating between host differences in medians of overall species richness determined by GLMMs with shared letters above plots indicating similar medians

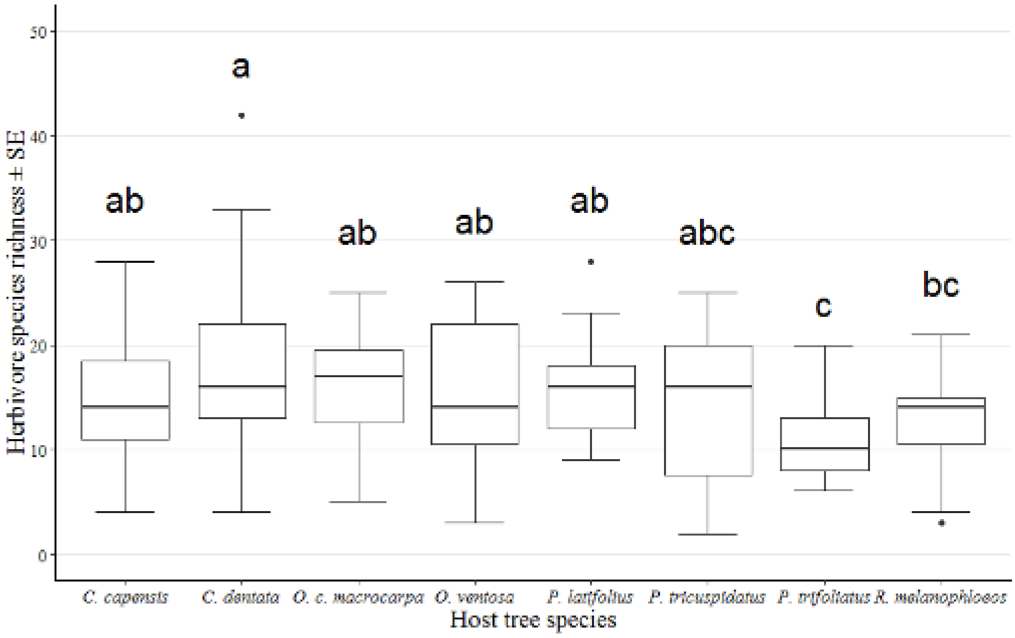

Figure S3: Box-and-whisker plots indicating between host differences in medians of herbivore species richness determined by GLMMs with shared letters above plots indicating similar medians

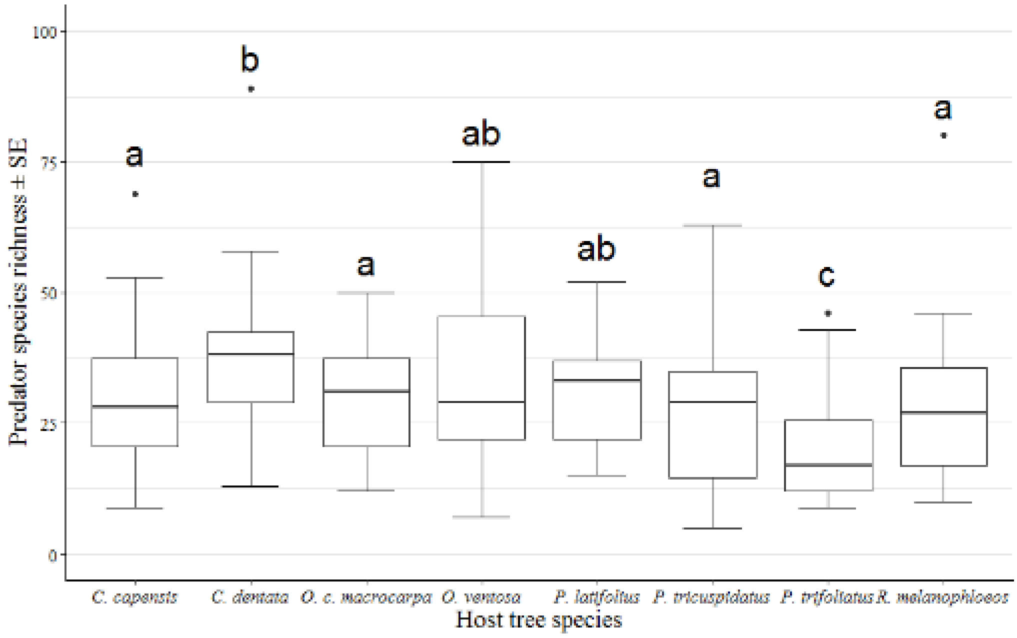

Figure S4: Box-and-whisker plots indicating between host differences in medians of predator species richness determined by GLMMs with shared letters above plots indicating similar medians

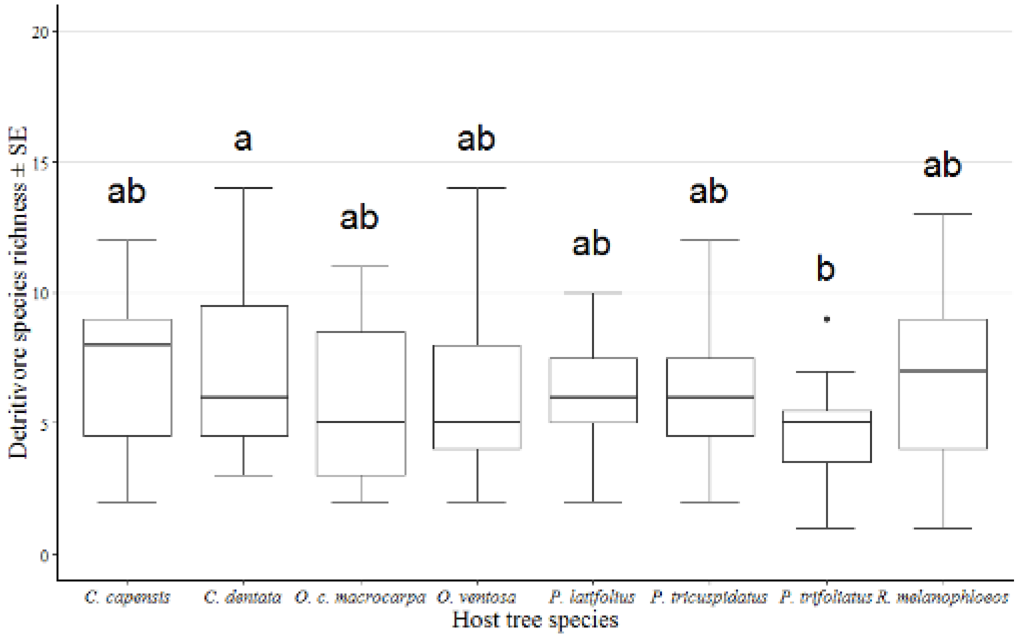

Figure S5: Box-and-whisker plots indicating between host differences in medians of detritivore species richness determined by GLMMs with shared letters above plots indicating similar medians

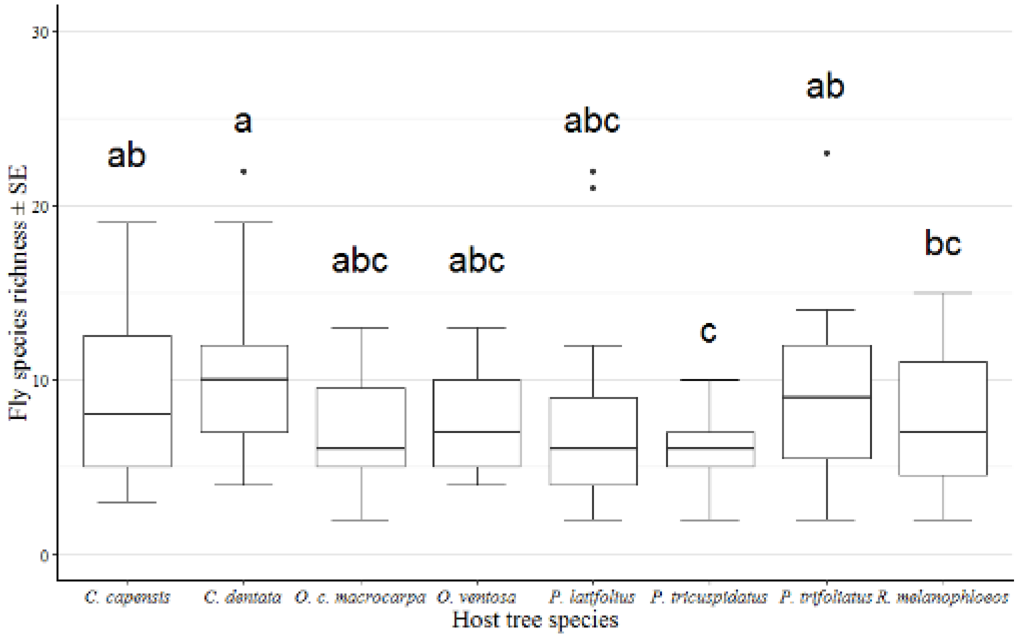

Figure S6: Box-and-whisker plots indicating between host differences in medians of fly species richness determined by GLMMs with shared letters above plots indicating similar medians

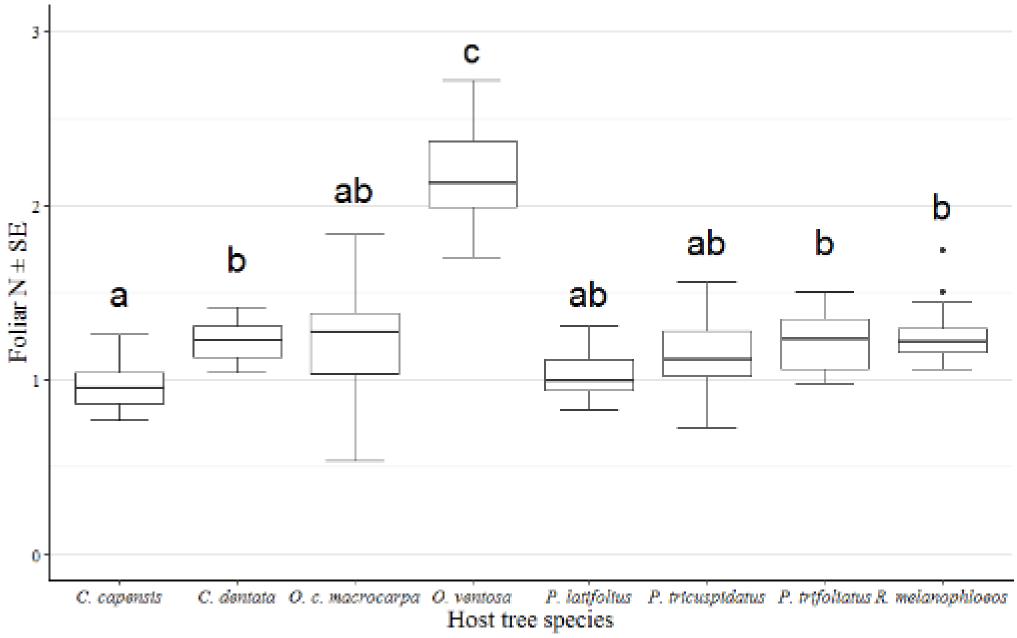

Figure S7: Box-and-whisker plots indicating between host differences in means of total foliar N content determined by LMMs with shared letters above plots indicating similar means

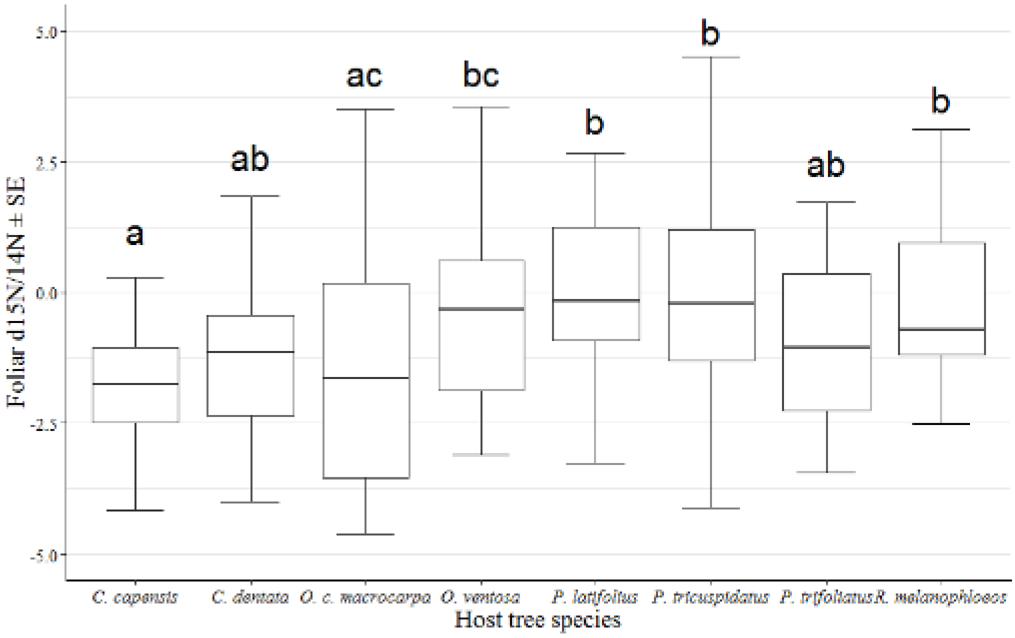

Figure S8: Box-and-whisker plots indicating between host differences in means of foliar δ15N/14N determined by LMMs with shared letters above plots indicating similar means

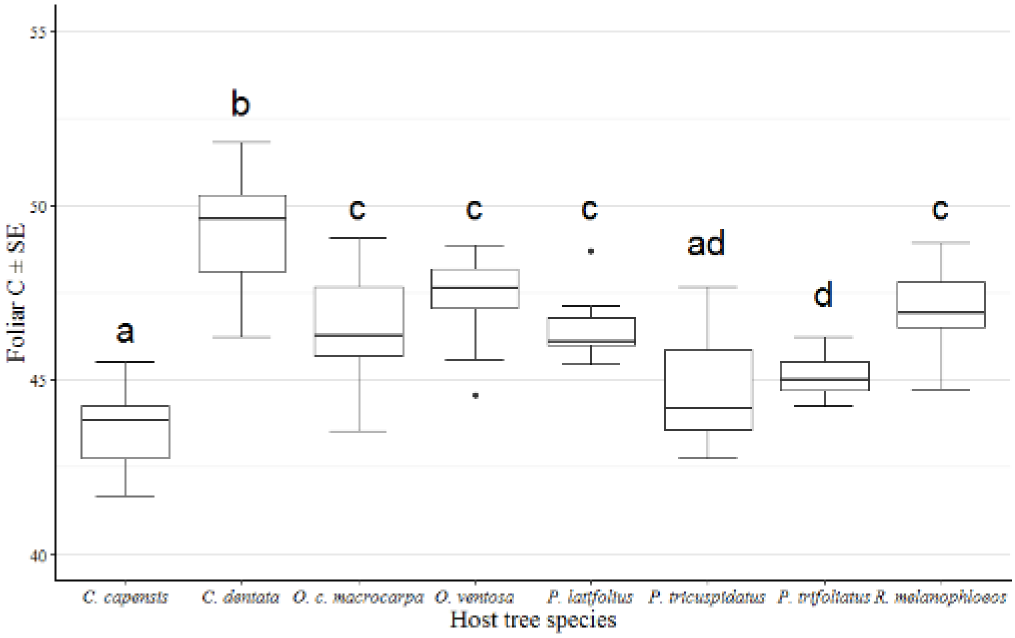

Figure S9: Box-and-whisker plots indicating between host differences in means of total foliar C content determined by LMMs with shared letters above plots indicating similar means

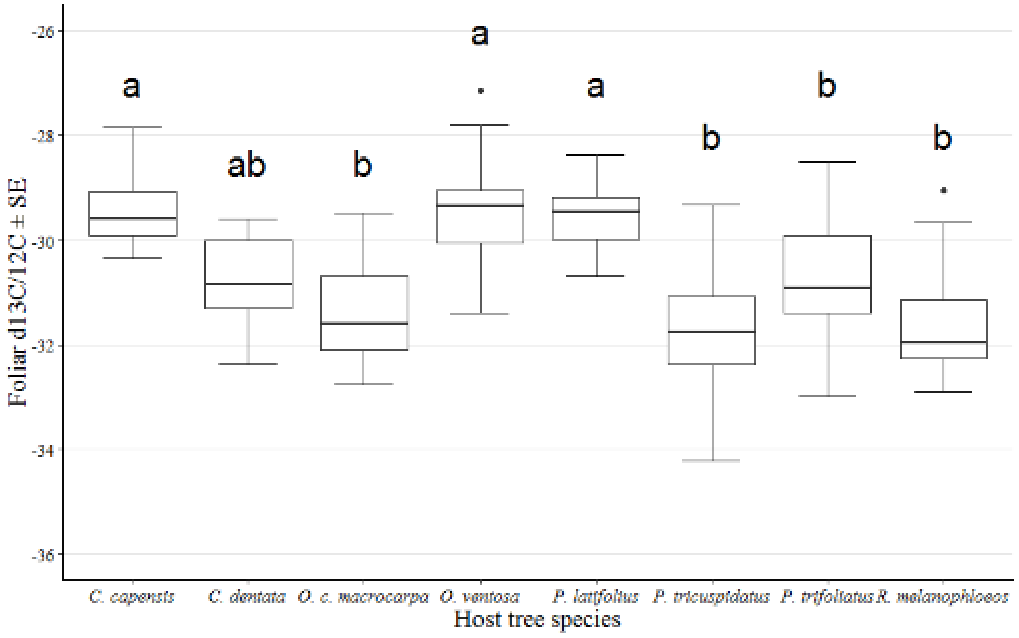

Figure S10: Box-and-whisker plots indicating between host differences in means of foliar δ13C/12C determined by LMMs with shared letters above plots indicating similar means

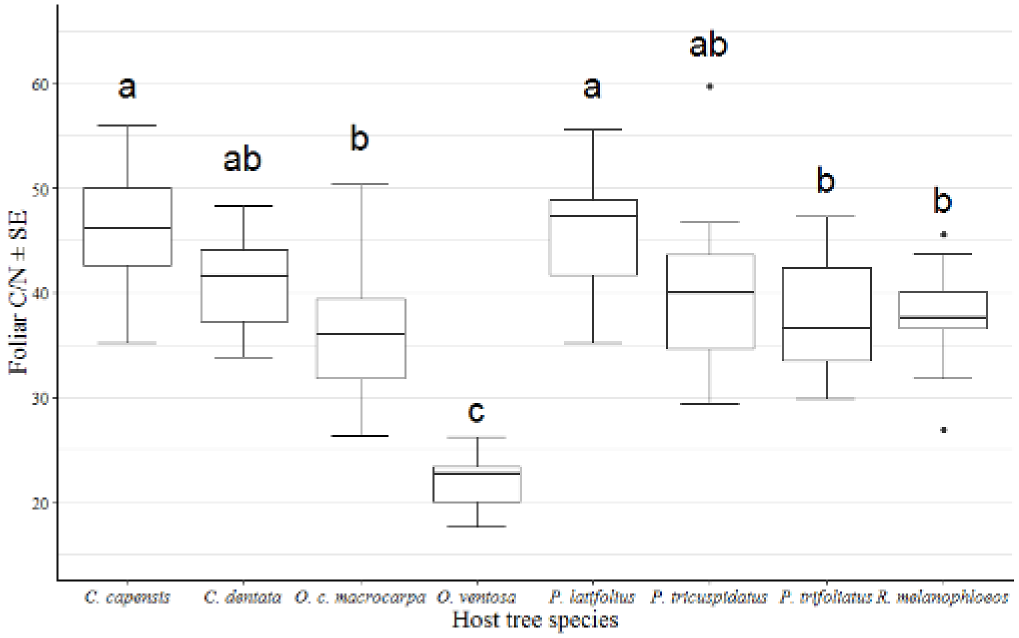

Figure S11: Box-and-whisker plots indicating between host differences in means of foliar C/N determined by LMMs with shared letters above plots indicating similar means

Chapter 5

Arthropods sampled from southern Afrotemperate forest canopies in a global perspective

Abstract

The biodiverse Afrotemperate forests on the south coast of South Africa are poorly known in terms of their invertebrate fauna. Globally, canopy fogging in forests point to beetles as being very rich in canopies. The aim here was to investigate the main canopy arthropod groups, with special emphasis on beetle diversity, collected from the canopies of various tree species in southern Afrotemperate forests. Against the tropical floristic affinity of these forests, I found that the canopy arthropod diversity was less than expected compared to canopy studies from tropical regions. With regards to beetles, these forests are more close to temperate than tropical regions in terms of species richness and richness per m², and are strikingly close to a Chilean temperate rainforest at a similar latitude. However, the most diverse beetle families sampled here, Curculionidae, Chrysomelidae and Staphylinidae, were similarly species rich in forest canopies from both temperate to tropical regions. The curculionids in particular were found to be highly diverse, similar to canopies elsewhere. I also show that different tree species and forest patches, support individualistic beetle assemblages despite being in the same region. Similar to some other canopy studies, hymenopterans here were overall more species rich even than beetles, supporting recent scientific quantifications of their global diversity. Our species estimates, and high numbers of undescribed species, justifies special conservation efforts to protect southern Afrotemperate forest canopies across the wide biogeographical gradient. Comparing my data here with earlier work, these forest canopies are ten-fold richer in arthropod species than the forest floors in this region.

Keywords: Arthropods; canopies; forest entomology; global diversity; tree canopy

Introduction

Forest canopies represent the interface between biodiversity and the atmosphere (Ozanne *et al*. 2003), and are globally recognised as biodiversity hotspots (Nakamura *et al*. 2017). Of the numerous species occurring within forest ecosystems, arthropods comprise a large part of total biodiversity. Erwin (1982) first drew attention to the great underestimation of global biodiversity after his pioneering work on canopy insect diversity in Panamanian tropical forests. From his conservative estimates, he concluded that there could be approximately 41 389 species per hectare of scrubby seasonal forest in Panama. He went further to suggest that there might be up to 30 000 000 species of tropical arthropods. Although these figures are only estimates and have since been challenged, they suggest that prior to 1982 we greatly underestimated the richness of global biodiversity. Currently, it is estimated that about 40% of extant terrestrial species globally occur within the forest canopy (Spence *et al*. 1997; Rodgers & Kitching 1998; Novotny *et al*. 2002), contributing greatly towards local and large-scale ecological integrity. Yet, despite this 'last biotic frontier' holding many biotic riches, it remains poorly understood, with large regional gaps (Nakamura et al. 2017). One reason for the relatively slow progress of canopy science is limited long-term access, with 22 continuous canopy access facilities globally (Nakamura *et al*. 2017). Fourteen of these facilities are in Europe, China, Japan and North America. Of the remainder, 4 are in South America, 1 in Papua New Guinea, 1 in Malaysia and 2 in Australia. The largest regional gap is Africa, which is not represented in the Canopy Crane Network, although hosting the world's second largest continuous rainforest after the Amazon, the Congo, and numerous other forests of potentially high value to science (i.e. Afromontane archipelago forests; White 1981).

Despite the limited number of canopy cranes globally, many alternative and shorter-term methods exist that can be used by researchers to study seemingly inaccessible areas. These include flight interception traps, hand-collecting, branch clipping, beating, sticky traps, canopy spraying and knockdown insecticide (i.e. canopy fogging) (Basset *et al*. 1997). The latter method is arguably the most well-known and most widely used, and was the method first popularized by Erwin (1982). It has quick implementation for short-term studies, collects large numbers of arthropods and creates 'clean' samples

(Basset *et al*. 1997). Importantly, it also produces samples related directly to specific tree individuals, and has good mobility (given still air conditions) to reach inaccessible areas. This method has been implemented the world over, but has been largely focussed around the tropics, Australasia, and in northern hemispheric temperate zones. The results from using this method often lead to new species discoveries, new estimates of global biodiversity and new admiration for the sheer numbers of arthropods inhabiting forest canopies (Basset 2001; Nakamura *et al*. 2017).

One large regional gap in canopy science are the forests that form part of the biodiverse Afromontane archipelago (sensu White 1981). The best-studied forests of this archipelago occur on the south coast of South Africa, forming a complex collectively classified as southern Afrotemperate forests (Mucina & Geldenhuys 2006). To understand the floral composition of these forests, it is crucial to understand the paleo-history of the region. During the Palaeocene (55-65 my BP), the southern tip of Africa was covered by mostly temperate forests of Gondwanan origin (Axelrod & Raven 1978; Deacon 1983). Examples of temperate tree lineages are still present today, and include the genera *Widdringtonia*, *Podocarpus*, *Cunonia* and *Platylophus* (Von Breitenbach 1974). During favourable climatic conditions in the Oligocene-Miocene, subtropical and tropical forests became dominant in the south-western Cape, by extending southward from continental Africa along river valleys and coastal plains, penetrating the original southern flora (Von Breitenbach 1974; Axelrod & Raven 1978; Deacon 1983). *Podocarpus latifolius* (Real Yellowwood), *Afrocarpus falcatus* (Outeniqua Yellowwood) and *Cunonia capensis* became dominant in mostly tropical forest communities (Von Breitenbach 1974; McKenzie 1978; Galley et al. 2006). However, despite the presence of temperate elements, the Oligocene-Miocene era was characterised by lowland and montane subtropical rainforest, with palms prominent (Coetzee 1978; 1983). Today, this vegetation type is absent in the region, although the southern Cape Afrotemperate forest complex is considered as impoverished remnants of former times (Coetzee 1978; 1983). Today, tropical tree lineages occur in both the southern Cape forests as well as in tropical Africa, and include *Apodytes dimidiata* (Icacinaceae), *Celtis africana* (Cannabaceae), *Diospyros whyteana* (Ebenaceae), *Kiggelaria africana* (Achareaceae) and *Rapanea melanophloeos* (Myrcinaceae) (Von Breitenbach 1974). Therefore, many genera of tropical origin today are prominent components of southern

Afrotemperate forests and, together with southern lineages, comprise the bulk of southern Afrotemperate forest tree diversity. Indeed, the similarities in genera between the Cape and areas as far north as Ethiopia follow the major mountain massifs (Grimshaw 2001). Also, the similarities with other southern hemispheric temperate rainforests are equally striking.

Despite Afromontane archipelago forests being of great value to science, little work has been done on their invertebrates, with only a few studies to date. Some seminal work include research on spiders from a Tanzanian Afromontane forest canopy (Sørensen 2003), and beyond the Afromontane archipelago, a report on spiders from tropical African forests (Seyfulina & De Bakker 2008). Beetle diversity from a Ugandan rainforest were described by Wagner (2000), who fogged 64 trees of four tree species, and Freund (2004) who studied leaf beetle diversity from Kenyan forest canopies. Other canopy studies in tropical Africa have focused on overall arthropods (Basset et al. 2001), ants (Schulz & Wagner 2002; Dejean et al. 2000), and homopterans (McKamey 1999). More work has been done on canopies in southern temperate rainforests, including on beetles from a temperate rainforest canopy in Chile (Arias et al. 2008; Richardson & Arias-Bohart 2011), ants from various temperate rainforest canopies in Australia (Majer et al. 2001), plecopterans from Valdivian forest canopies in southern Chile (Shepard & Baumann 2011), and overall arthropods from canopies of Tasmanian southern temperate beech forests (Keble-Williams 2012) and New-Zealand *Podocarpus*-hardwood forests (McWilliam & Death 1998). Some research on arthropods have also been conducted in forest canopies in New Caledonia (Guilbert 1998).

From these and many other studies involving canopy fogging in forests across the globe, one of the consistently super rich insect groups are the beetles (Basset 2001; Novotny & Basset 2005; Nakamura et al. 2017). Describing and monitoring beetle diversity in canopies provide much information on their interactions with trees, and might be used to assess threats stemming from climate change (Spinoni et al. 2017). From the highly diverse, sunlit forest canopy moving down towards the damp, shaded forest floor, beetles have colonised almost every available microhabitat. Their role as a group in upholding forest ecosystems is, arguably, unmatched compared to other animals. In one season, an outbreak can decimate vast expanses of forest trees (i.e. mountain pine beetle in Canadian forests, Taylor et al. 2006), whereas in another season, beetles might pollinate an equally vast expanse of forest flora (Irvine & Armstrong 1990), ensuring its survival. These extremities are, however, minuscule compared to infinite, and often ecologically sensitive interactions, ranging from antagonistic to mutualistic, that beetles form with trees and other biota on a daily basis, and so maintain forest integrity.

The aim here is to provide, for the first time, a synthesis of the arthropod diversity collected from the canopies of various tree species in southern Afrotemperate forests, South Africa, by means of canopy fogging, and to compare this to other forest systems around the world. Special emphasis is placed on the beetle fauna, which is a well-studied canopy group globally allowing for good comparisons. Firstly, I provide a summary highlighting the arthropod taxonomic diversity, by focussing on the dominant arthropod groups present. Then, I discuss beetle diversity by investigating both global patterns as well as regional patterns. Lastly, I discuss the dominant arthropod taxa sampled, in order from most to least abundant.

Materials and Methods

This study was conducted in southern Afrotemperate forests in the Greater Cape Floristic Region of South Africa, in the largest forest complex in the country. Globally, these forests have the greatest tree diversity of warm temperate forests, unmatched in the southern hemisphere, despite covering a relatively small surface area (Silander 2001). Moreover, the diversity of plant genera and families is unrivalled in relation to size (Silander 2001; Cowling & Lombard 2002). This forest complex has a naturally fragmented distribution, and consists of more than 1500 separate natural forest patches, of which most are between 1-50 hectares, with only 15 forests being larger than 800 ha (Berliner 2009). Five forest patches, between 200 and 504 ha in size, were selected here. These occur on a west-east gradient, with the most westerly forest, Oubos, being 390 km from the most easterly forest, Witelsbos. These forests gradually increases in plant species richness, and temperature, moving west to east (Geldenhuys & MacDevette 1989; unpublished data). The five forests were chosen based on distances between patches, as well as patch size (Table 1; Fig. 1 – chapter 4).

The most westerly site, Oubos, is isolated at the southern ridges of the Riviersonderend Mountains, separated from the nearest mountains on which the other four forests by a valley of ± 15 km. The other four forests occur at the southern slopes of a long, west-east running mountain range, the Langeberg Mountains. The two most westerly forest patches occur in a winter-rainfall landscape, the central patch in a transition zone between winter- and summer rainfall, with the two easterly sites occurring in a summer rainfall region (WCDoA 2019). Therefore, although these forests are all temperate with regards to latitude, there is a gradient from strictly temperate to increasingly subtropical landscapes eastward. Indeed, although annual rainfall patterns are largely similar within the five forest patches, largely due to topography and elevation, the rainfall patterns of the surrounding landscapes are not.

We obtained daily temperature data using ibuttons (Dallas semiconductors, USA) over three months during the spring/early summer (Aug-Oct; unpublished data), of which two were placed in each forest under dense tree crowns. There was a mean 1.65 C° increase in mean temperature from west to east (Oubos = 14.35 C° ± 5.3 C°; Witelsbos = 15.9 C° ± 5.1 C°).

Table 2: List of 5 forests included in this study with their respective size, elevation and location

Forest	**Size (±)**	**Elevation**	**Coordinates**
Oubos	381 ha	390 m	-34.07, 19.82
Grootvadersbosch	357 ha	370 m	-33.98, 20.80
Kleinbos	200 ha	410 m	-33.93, 22.13
Woodville	504 ha	260 m	-33.93, 22.62
Witelsbos	379 ha	250 m	-33.98, 24.10

Arthropod sampling

The detailed procedure of arthropod sampling that was followed is set out in chapter 4 of this thesis, with details on each forest provided in chapter 1. In short, arthropods were sampled using chemical fog released from the ground. One-hundred-and-twenty (120) individual trees were fogged over the two summer months of January and February 2017. These tree individuals were equally divided into eight tree species, equating to 15 individuals per species and three individuals of each species per forest patch. These species are common components of southern Afrotemperate forests. A brief description of each species is given in the supplementary material, Text S1.

All arthropods collected were classified to at least the order level, and assigned to morphospecies. Larvae and immature individuals were excluded. Spiders and ants were, where possible, identified to species level by taxonomic experts from the University of Pretoria (A.S. Dippenaar-Schoeman; C. Haddad) and SANParks scientific services (M. De Mornay) respectively. Hymenopterans are currently housed for future taxonomic revisions at the Iziko Entomology Museum in Cape Town (S. Van Noort). Hemipterans and beetles were identified to family-level at the Conservation Ecology and Entomology Laboratory in Stellenbosch using field guides and keys (Scholtz & Holm 1985; Picker et al. 2004), and flies and all other arthropods to order level. A reference collection of morphospecies is housed at the Entomology Museum, Stellenbosch University, with the exception of the spiders (South African National Collection of Arachnida, Pretoria), ants and wasps (Iziko Entomology Museum, Cape Town).

Statistical analyses

Species estimates for the six dominant taxonomic groups were obtained using Chao2 and Jacknife2 procedures in PRIMER 6 (Clarke & Gorley 2006). These included the hymenopterans, beetles, flies, bugs, spiders and ants, from most speciose to least speciose. To determine differences in assemblage composition of beetles sampled between the forest patches, as well as between the various forest tree species, I used Permutational Multivariate Analysis of Variance (PERMANOVA), applied to square-root transformed data, using Bray-Curtis similarity matrices. These were subsequently visualized using a CAP-analysis, using the same statistical package, PRIMER 6 (Clarke & Gorley 2006). A dendrogram, indicating percentage similarities in beetle assemblages between tree species, using average group Bray-Curtis similarity matrices, was created in the same statistical programme. For this, replicate trees per species (n = 15) were combined to achieve a composite assemblage for each species (Gering & Crist 2000). To examine the relationship between host tree genotype and associated beetle diversity, I firstly determined genetic distance (DNAdist) between the eight host trees using the programme Chromas 2.2.6 (Tecnelysium Pty Ltd). Average similarities in assemblage composition of beetles, obtained as described above, were plotted against genetic distance through the package *ggpubr* in R (Kassambara 2017). A Spearman rank correlation coefficient were then calculated, (together with a p-value at 5% significance), to determine significance of correlations, in the same R package.

Global comparisons

Firstly, I report the diversity found in the current study, and then compare the broad findings with other canopy studies across the globe. Secondly, relevant scientific publications (only those which implemented fogging/spraying by means of chemical knockdown insecticide and that focussed on beetles) were then studied in terms of latitude of the study region, number of trees and species sampled, and the sampling area underneath the host trees. Due to the different methods, data obtained are difficult to directly compare between individual trees, stemming mainly from the sampling area placed underneath focal trees, as well as tree size and foliage density, both of which show great variability between studies. I therefore compare beetle richness per 1 m^2 of sampling sheets/funnels, similar to Wagner (2000), which allows for more direct comparisons as opposed to between individual trees.

The two arthropod groups that were identified lower than the family-level, spiders and ants, are compared to other global publications in tables. This I did by listing the dominant families/subfamilies/genera (depending on the group) between different regions, i.e. temperate vs. tropical, obtained from the literature, compared to the findings here. The remaining dominant groups, the wasps, flies, and bugs, are briefly discussed.

Results and discussion

The order of the results and discussion section follows the absolute abundances of the top six diverse arthropod groups, following a brief overview of the overall diversity patterns found.

Overall diversity patterns

In total, 20 734 arthropod specimens were sampled here, comprising 1 522 species. Estimates of species richness were placed at 2 602 (± 111.75) and 2706, for Chao2 and Jacknife2 estimates respectively (Table 2). Beetles were the most abundant taxon, followed by wasps and flies (Table 2). The most species rich taxon was hymenopterans (excluding ants), with 472 species. Beetles comprised 321 species. Other species-rich groups were the flies, bugs (hemipterans), and spiders, with richness of 211, 129 and 90 respectively (Table 2).

Table 3: Overall and top six diverse arthropod taxa sampled from southern Afrotemperate forest canopies ranked according to their absolute abundance including species richness estimates

Taxon	**Abundance**	**Sampled Richness**	**Chao2 (± SD)**	**Jacknife2**
All arthropods	20 734	1522	2602 ± 111.75	2706
Beetles	4887	321	553.73 ± 50.71	583.37
Hymenopterans	2856	472	795.71 ± 58.71	845.29
Flies	2642	211	383.27 ± 47.22	387.17
Spiders	2388	90	100.23 ± 6.90	108.9
Bugs	2166	129	239.25 ± 39.46	235.87
Ants	1178	36	78.66 ± 33.23	64.67

Compared to many other global canopy studies, these forests had low levels of arthropod diversity. For example, richness of beetles in tropical areas would often far exceed numbers reported here (Basset 2001). We sampled 41 (± 3.25) beetles with a mean 13 (± 0.63) beetle species per tree, across host species, with the highest beetle richness from any individual tree (*C. dentata*) being 38. Allison et al. (1997) reported a mean number of beetle species per tree of 113 in tropical Papua New Guinea. From a Chilean temperate rainforest at a near similar southern latitude as our study region, average beetle richness per tree was 54 (Arias et al. 2008). Our results are more similar to northern temperate regions at similar latitudes, for example a temperate deciduous forest from Ohio, had mean beetle richness ranging between 10 and 20, depending on the tree species (Gering & Crist 2000). Thus, we confirm the results from a comparative study between Britain and South Africa, which included six tree species and their canopy fauna, in which the average indices of diversity were similar between the regions (Moran & Southwood 1982). They further concluded that South African arthropod fauna are fewer, but larger, than those sampled in Britain (Moran & Southwood 1982). This is despite the fact that South Africa did not undergo glaciation during the previous glacial maxima, as northern temperate forests undoubtedly would have (Clark et al. 2009), providing an interesting conundrum, perhaps explained by forest size.

Northern temperate forests far exceed South Africa’s forests in size. That southern Afrotemperate forests are relatively small compared to forests included in other fogging studies, and have relatively low levels of canopy arthropod diversity, relates to the island biogeography theory (Losos & Ricklefs 2010; Yekwayo et al. 2016). The natural distribution of these forests are disjunct, comprised of numerous naturally-small patches, mostly 1-50 ha. Still, these are the largest forests in South Africa at over 60 000 ha as a combined total (Geldenhuys 1991), naturally sustained largely by fire interacting with topography. From a global perspective, these are very small, scattered and isolated as islands within a broader, low-vegetation landscape consisting of fynbos, as well as today, transformed areas (Swart et al. 2018). Evidently, this forest system is very different from forests of other southern and northern temperate regions, which are often continuous and dominant landscape features in their natural state, i.e. the southern forests of Chile (Veblen et al. 1996), New-Zealand (Wardle & Coleman 1992) and temperate Australia (Wood et al. 2010).

Beetles

Beetle diversity in a global context

The beetles are arguably the best studied arthropod group in tree canopies, and also one of the most diverse. In total, I sampled 321 species of adult beetle from southern Afrotemperate canopies, totaling 4 887 specimens. Compared to tropical regions, such as a rainforest in Uganda, which revealed 1433 beetle morphospecies from 64 trees fogged (Wagner 2000), the total beetle diversity reported here is much lower, but slightly higher compared to canopy studies from North America (272 spp., Gering & Crist 2000) and Britain (144 spp., Stork et al. 2001). From a study where 50 oak trees were fogged over two years in the United Kingdom, 202 beetle species were sampled (Stork & Hammond 1997). Different sampling efforts and methods necessarily affect outcomes, and species estimates are therefore better for comparative purposes. Using Chao2 and Jacknife2 estimates of beetle richness, revealed an estimated beetle richness in southern Afrotemperate forest canopies respectively of 553.73 (± 50.71) and 583.37 (Fig. 1), with species estimates not reaching an asymptote. This is strikingly comparable to southern temperate rainforests in Chile (estimated 600+ spp., Arias et al. 2008), which included tree taxa from Gondwanan origin, similar to the current study.

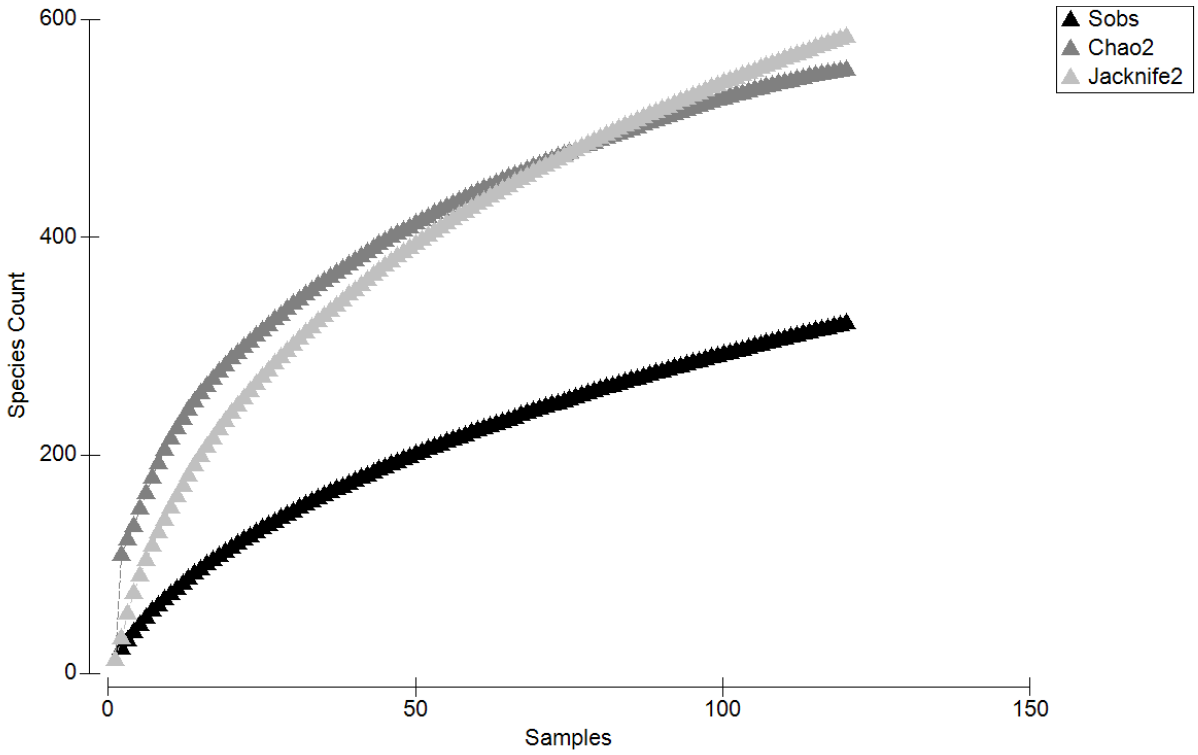

Figure 1: Species estimates shown by means of an accumulation curve indicating observed beetle richness (Sobs), Chao2 species estimates (dark grey) and Jacknife2 estimates (light grey).

Here, the most species-rich family was Curculionidae, totaling 46 species. This was followed by Chrysomelidae (30) and Staphylinidae (30), with Carabidae having a richness of 26 species. In terms of abundance, Curculionidae was also the most abundant beetle family sampled (312), followed by Chrysomelidae (237) and Coccinellidae (142) (Fig. 2).

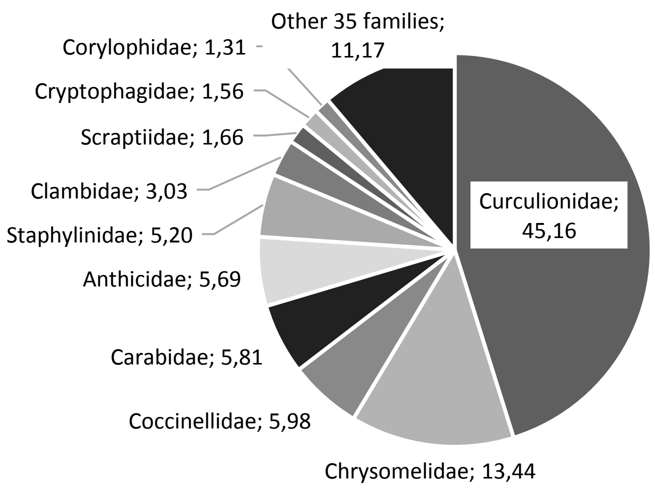

Figure 2: Proportion of 10 most abundant beetle families in terms of total abundances across all sites and tree species in %

Curculionidae, the most speciose family here, is well represented in many forest canopies globally, and was the most species-rich beetle family from tropical Amazonia (Erwin 1982), temperate North-America (Gering & Crist 2000), subtropical Australia (Basset 1991) and temperate Chile (Arias et al. 2008) (Table 3). Evidently, the weevils are one of the most species-rich families in forest canopies globally (Basset 2001).

From a Ugandan tropical forest, canopy beetles were more diverse than reported here, with vastly different taxonomic composition (Wagner 2000). For example, Wagner (2000) reported the most species rich family to be Latridiidae, and the most abundant Staphylinidae. Curculionidae were only the 5th most abundant family, and the 2nd most species rich (Wagner 2000). Despite being on the same continent, our results are in strong accordance rather with other global canopy studies ranging from temperate to tropical, in which the families Curculionidae, Chrysomelidae and Staphylinidae are typically the most abundant and species rich (Basset 2001; Table 3). Geographical proximity therefore does not necessarily determine similarities in beetle families in forest canopies.

The 321 species consisted of 45 beetle families (Scolytinae treated as family for comparative purposes). Erwin (1983) reported 57 beetle families from Brazil, treating Scolytinae as a separate family, while also sampling five unidentified families. Basset (1991) similarly treated Scolytinae as a separate family, and reported 53 beetle families from subtropical Australian tree crowns. From temperate Chile, fogging tree canopies revealed 54 beetle families (Arias et al. 2008). From North American old-growth forest canopies, 40 beetle families were sampled, with nine species identified from unknown families (Gering & Crist 2000). Marques et al. (2006) found 32 beetle families trees of the Brazilian Pantanal, although relatively few tree individuals were sampled. At least for canopy beetle families, southern Afrotemperate forests are seemingly less diverse than tropical, subtropical, and southern temperate regions, but more diverse than northern temperate forests.

Table 4: Comparison between selected results using canopy fog sampling of beetles from various localities across the globe (blank = not reported in publication).

Publication	**Area**	**Region**	**Tree species and amount (n)**	**Abundance**	**Richness**	**Most abundant family**	**Most species rich family**
Erwin & Scott (1980)	Panama	Tropical	*Luehea seemanni (19)*	7 712	945+	Chrysomelidae	Chrysomelidae
Southwood et al. (1982)	South Africa	Subtropical	*Erythrina caffra (3)*		58		
Southwood et al. (1982)	South Africa	Subtropical	*Quercus robur (3)*		34		
Southwood et al. (1982)	Britain	Temperate	*Quercus robur (3)*		53		
Erwin (1983)	Central Amazonia	Tropical		24 350	1 080		Curculionidae
Stork (1988; 1991)	Borneo	Tropical	Several trees *(10)*		±840		
Basset (1991)	Brisbane, Australia	Subtropical	*Argyrodendron actinophyllum (10)*	863	68	Chrysomelidae	Curculionidae
Allison et al. (1993)	New Guinea	Tropical	Several trees *(8)*	4 840	633		Curculionidae + Staphylinidae
Allison et al. (1997)	New Guinea	Tropical	*Castanopsis acuminatissima (8)*	3 977	418	Staphylinidae	Chrysomelidae + Staphylinidae
Gering & Crist (2000)	Ohio, USA	Temperate	Several trees *(4)*	1 459	272	Curculionidae	Curculionidae
Wagner (2000)	Uganda	Tropical	Several trees *(64)*	29 736	1 433	Latridiidae	Staphylinidae
Marques et al. (2006)	Pantanal, Brazil	Tropical	*Vochysia divergens (3)*	2 197	256	Nitidulidae	Chrysomelidae
Stork & Grimbacher (2006)	Cairns, Australia	Tropical		14 473	1 158	Curculionidae	
Ulyshen & Hanula (2007)	Georgia, USA	Temperate	Several trees *(12)*	15 102	558	Lathridiidae	Cerambycidae
Arias et al. (2008)	Chile	Temperate	Several trees *(29)*	25 497	485	Curculionidae	Curculionidae
Stork & Hammond (2013)	Britain	Temperate	*Quercus robur (3)*	5 613	150	Coccinellidae	
Swart et al. (this study)	South Africa	Temperate	Several trees *(120)*	4 887	321	Curculionidae	Curculionidae

Comparison of the literature on canopy fogging studies, revealed a general decrease in beetle diversity per m² of canopy fogged with increases in latitude (Fig. 3). Some canopy studies from the tropics, however, revealed levels of beetle richness per m² similar to those reported here, including findings from Uganda (Wagner 2000) and Sulawesi, Indonesia (Hammond 1997). These seems to be outliers regarding the general trend (Fig. 3). Indeed, beetle richness from the eight tree species included here are well placed in a temperate context, albeit less diverse than previous results from tree canopies in South Africa and even the UK (Southwood et al. 1982). When leaving aside the two tropical outliers, beetle richness per m² in southern Afrotemperate forests fall within the range between a subtropical tree near Brisbane, Australia (Basset 1991) and Gondwanan relict trees from temperate Chilean rainforests (Arias et al. 2008) (Fig. 3). Despite the tropical affinity of southern Afrotemperate forests, the beetle richness therefore is closer in terms of latitude than paleo-history of the region. Most (5/8) of the tree species here have Gondwanan links as in Chile (Arias et al. 2008). These five species do not seem to differ in beetle richness compared to trees of a historically tropical origin in the same region, as all eight tree species revealed a diversity comparable to other temperate regions.

Importantly, figure 4 should be analysed in context of the methodology used. The outlier for the temperate canopy studies, for example (re: Britain, Southwood et al. 1982), represents beetle richness from three individuals of *Quercus robur*, and although seemingly more diverse per m², revealed considerably less beetle richness overall (53 spp.) compared to the results reported here (81-104 spp. for the respective tree species).

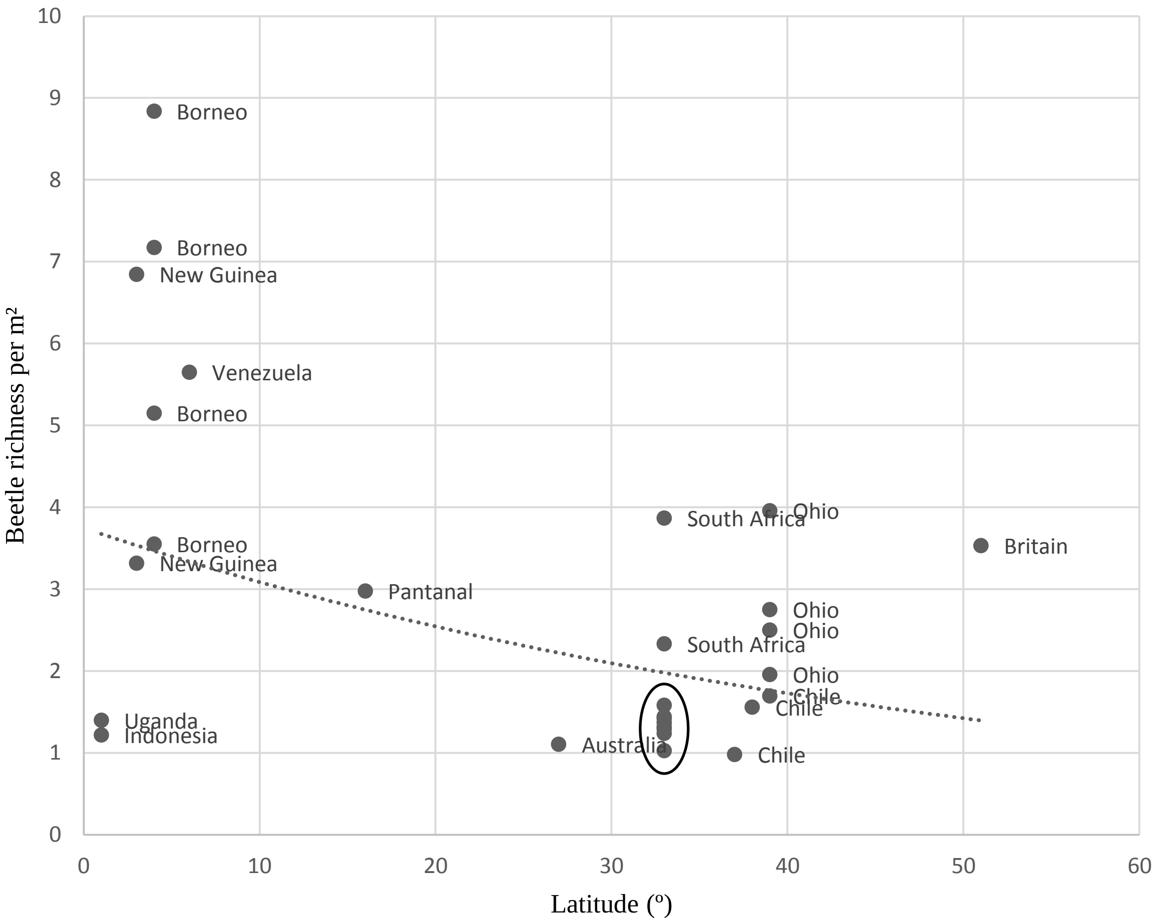

Figure 3: Relationship between latitude and beetle species per square metre sampled from canopy fogging for various tree species (data obtained from various publications; for details see supplementary material, Table S2) with the study regions indicated. Circled points represents the eight tree species sampled from southern Afrotemperate forest canopies in the current study.

Beetle diversity between forest patches

Although canopy sampling was done from the same eight tree species ranging across the five forest patches, beetle assemblage composition in each were significantly different between the forest patches when pooled ($P < 0.001$; Fig. 4). Grootvadersbosch followed by Oubos, the two most westerly forest patches, revealed the most separate beetle assemblages, with, conversely, greater overlap between Kleinbos and Woodville, the forest patches nearest each other. The most easterly site, Witelsbos, showed some overlap with the other forest patches. However, overall it had very different beetle assemblage composition (Fig. 4). Evidently, proximity to nearest forest patch within this region explains variation in beetle assemblages, indicating isolation of forest patches from a once larger forested region

(Geldenhuys 1997), and/or limited dispersal capabilities of beetles over longer distances (Baselga et al. 2012).

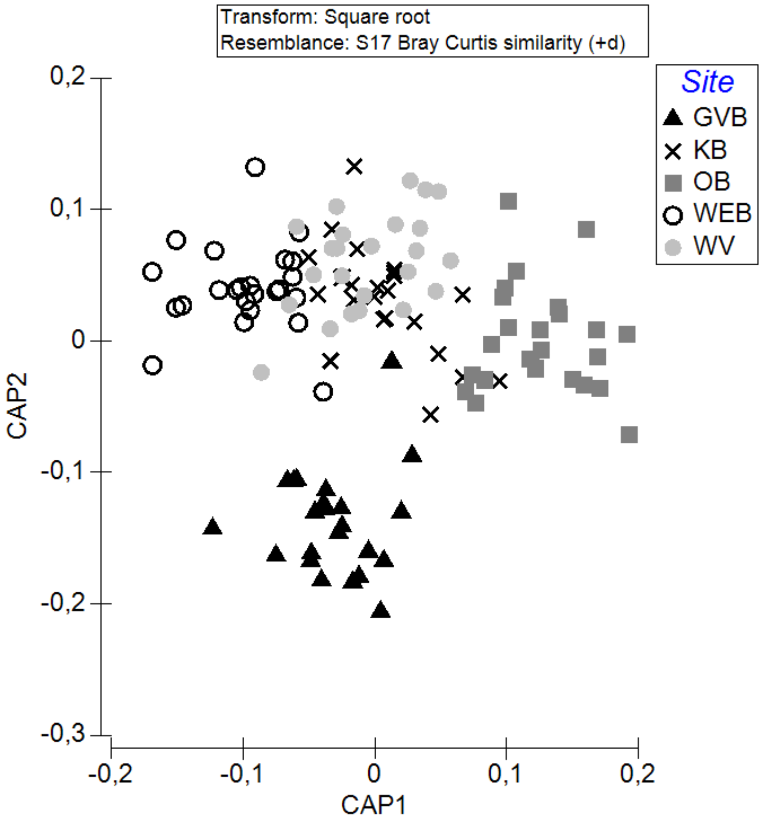

Figure 4: CAP analysis based on Bray-Curtis similarity indicating the various forest patches and the beetle assemblages sampled from their canopies. OB = Oubos, GVB = Grootvadersbosch; KB = Kleinbos; WV = Woodville; WEB = Witelsbos.

The forest with greatest beetle species richness and number of beetle families was Woodville (Table 4). This forest is the largest studied here, compared to the other forests, and connected to the largest indigenous forested area in the region, and the country. Woodville had six more beetle families and 50 more beetle species compared to Grootvadersbosch, a relatively small and isolated forest patch. Woodville forest is not the warmest forest, nor does it have the lowest elevation or the highest plant diversity. The only distinguishing factor of this forest compared to the other forests here, is its size, connectedness, and closeness to a much larger forest. Therefore, we propose that the greater beetle diversity here is explained by traditional island biogeography theory (Losos & Ricklefs 2010; Yekwayo et al. 2016), with larger patches having higher richness relative to smaller patches (Fig. 5). This was also found for the number of families, which increased with patch size. Interestingly, abundance revealed a converse relationship between numbers of individuals and patch size (Fig. 5).

Table 4: Diversity statistics for beetle fauna sampled from various tree canopies over a west-east gradient

Site	Longitude	Patch size	No. of trees fogged	Abundance	Species richness	No. of families
Oubos	19.82	381 ha	24	961	110	31
Grootvadersbosch	20.80	357 ha	24	636	96	28
Kleinbos	22.13	200 ha	24	1320	134	30
Woodville	22.62	504 ha	24	1006	146	34
Witelsbos	24.10	379 ha	24	964	113	31
Total			120	4887	321	45

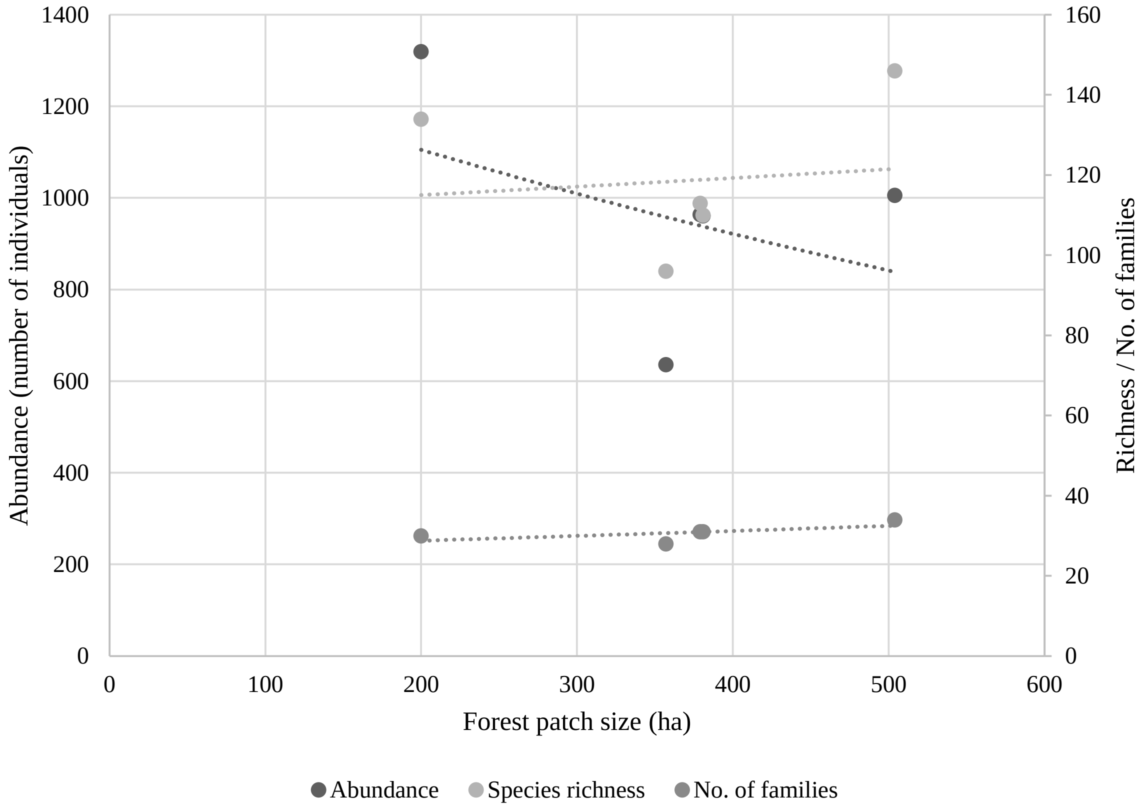

Figure 5: The correlation between patch size and beetle diversity indices, including abundance, richness and no. of families for each of the five forests.

Beetle families showed different patterns with regards to landscape-level features. Here, Woodville had highest weevil species richness (22 species), and the lowest richness was sampled in the most easterly site (10 species) (Supplementary material, Table S3). Landscape level patterns did not reveal any west-east gradient for species richness, nor for abundance, for the weevils. The noticeable drop in weevil abundances in Grootvadersbosch (Supplementary material, Table S3), seems to be replaced by an increase in numbers of chrysomelids.

Chrysomelidae and Staphylinidae were the second most speciose families. Other publications on tropical and subtropical regions report high levels of chrysomelid diversity (Erwin & Scott 1980; Basset 1991), with relatively lower levels in temperate canopy studies (Spence et al. 1997). In Panama, Erwin & Scott (1980) found the most species rich beetle families from a single tree species, *Leuhea seemmani*, to be Chrysomelidae, Staphylinidae, Cerambycidae, Mordelidae and Carabidae. In a subtropical forest near Brisbane, fogging of the tree species *Argyrodendron actinophyllum* showed the most dominant coleopteran families to be, from highest to lowest, Chrysomelidae, Scolytidae, Corylophidae, Staphylinidae, and Curculionidae (Basset 1991). Proportionately, chrysomelids only contributed to 3.54% of total beetle catches in Oubos, compared to 31.92% in Grootvadersbosch. This is an interesting pattern, as forests east of Grootvadersbosch show proportional decreases in chrysomelid abundance. However, this could be ascribed to relatively lower beetle diversity sampled from Grootvadersbosch (Supplementary material, Table S3). Despite the high abundance of chrysomelids in Grootvadersbosch, species richness was less than half of the other forests.

Staphylinidae species richness and abundance showed noteworthy west-east patterns. For richness, a near linear increase was witnessed, with the most westerly site hosting seven species, followed by 9, 13, 16 and 15 for the forests moving east, respectively, more than doubling the diversity over this gradient. Abundance, too, showed a similar pattern, with the most westerly site having the lowest numbers of staphylinids. Two species of staphylinid, C131 and C79, only occurred in the three most easterly forests, yet species C69 and C190 were found in all forests except the most westerly site. Perhaps, warmer and more florally diverse forests provide conditions for more staphylinid species, with their wide range of feeding strategies, predatory, fungivorous, and scavenging (Basset 2001), with many micro-habitats to exploit.

The most abundant predator family here was Coccinellidae (292). In terms of both its abundance and species richness, coccinellids were relatively more diverse in the three eastern forest patches compared to the two western forest patches (Supplementary material, table S3). From the rainforest tree *Leuhea seemanii*, Panama, coccinellids were poorly represented, compared to temperate ecosystems where they are generally well represented (Basset 1991). However, in tropical Borneo, coccinellids was the fourth most species-rich beetle family (50 spp.), after Curculionidae (337 spp.), Chrysomelidae (170 spp.) and Tenebrionidae (57 spp.) (Stork 1988), indicating that even between tropical ecosystems across continents, there are great differences.

Beetle diversity between host species

Only two tree species had a beetle richness equal to or exceeding 100, *O. c. macrocarpa* (104 species) and *C. dentata* (100 species) (Table 5). *Olea capensis macrocarpa* also had the highest number of beetle families (30). However, in terms of abundance, *O. ventosa* hosted the highest number of sampled beetles mainly due to an abundance of morphospecies C5 (Coleoptera: Curculionidae). The number of families ranged between 25 and 30 (Table 5).

Table 5: Summary statistics of total canopy beetle diversity between eight tree species

Species	No. of trees fogged	Abundance	Species richness	No. of families
C. dentata	15	723	100	29
C. capensis	15	564	87	27
O. ventosa	15	888	88	25
O. c. macrocarpa	15	595	104	30
P. latifolius	15	710	97	28
P. tricuspidatus	15	485	99	27
R. melanophloeos	15	462	88	29
P. trifoliatus	15	460	81	27

The most disparate beetle assemblage, as determined by PERMANOVA in PRIMER 6 (Clarke & Gorley 2006), were sampled from *P. latifolius* canopies and *C. capensis* canopies respectively (Fig. 6).

Both tree species are viewed as Gondwanan relicts. Our results suggest that evolutionary histories of tree species is important in determining its associated beetle fauna, as the only two species sharing a family, *P. trifoliatus* and *C. capensis*, were more closely related to each other in terms of percentage similarity of beetle fauna compared to the other tree species (Fig. 7). However, genetic distance between host species did not correlate with beetle assemblage similarity (Spearman rank correlation coefficient = 0.31, p > 0.05; Fig. 8). However, many arthropod species remain undersampled in fogging events, due to wind drift, or entanglement in branches and leaves (Dial et al. 2006). To date, no study has assessed these drawbacks in fogging studies, which could affect reported results. Also, to effectively delineate beetle composition on host tree species with genetic similarity, having information on beetle specialists versus generalists will be important.

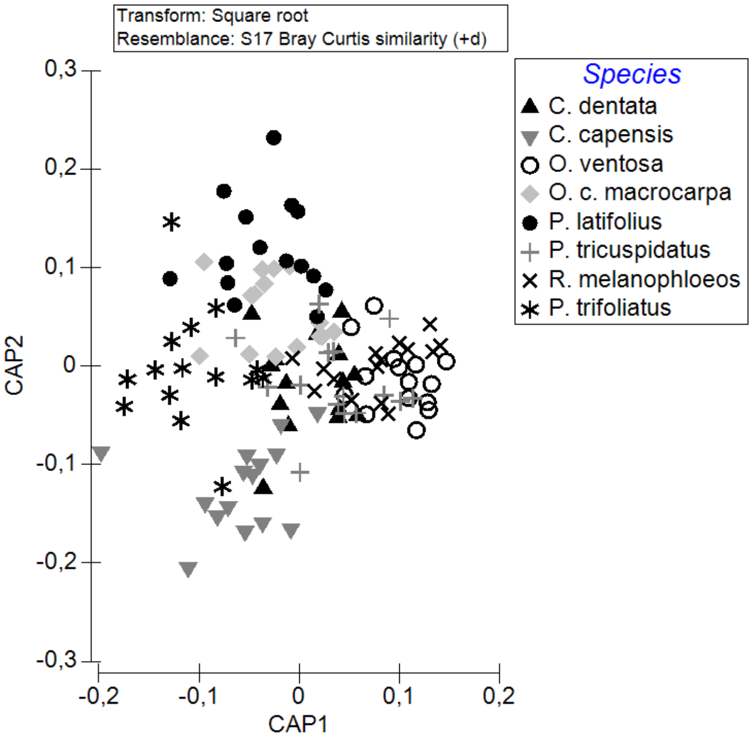

Figure 6: CAP analysis based on Bray-Curtis similarity indicating the various tree species and the beetle assemblages sampled from their canopies.

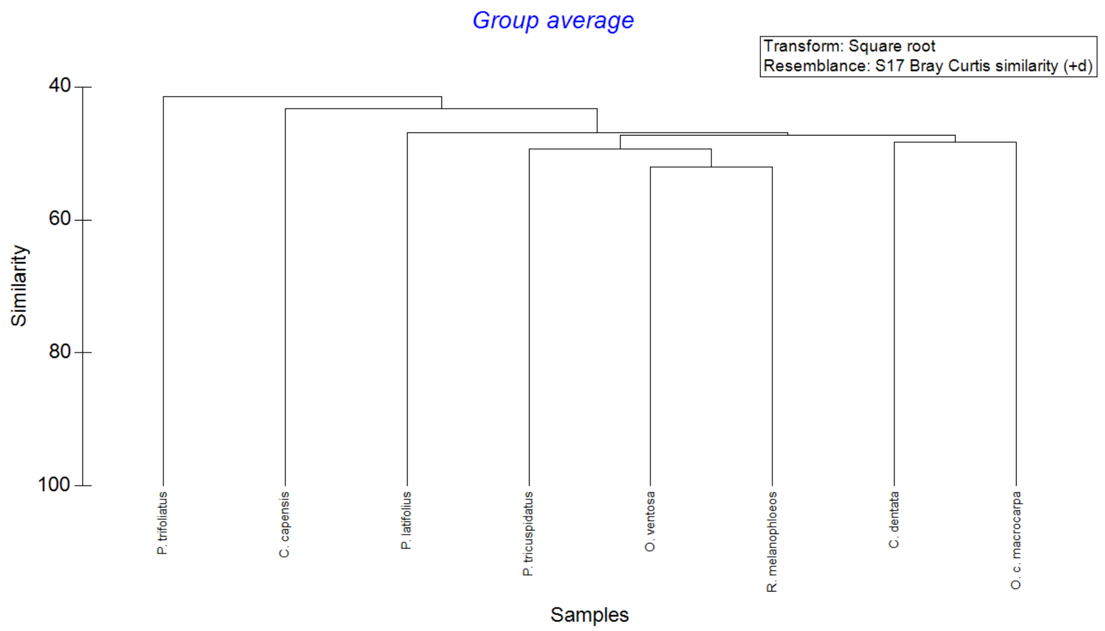

Figure 7: Dendogram indicating percentage similarities in beetle assemblages using average group Bray-Curtis similarity matrices. Replicate trees (n = 15) were combined to achieve a composite assemblage for each species (Gering & Crist 2000).

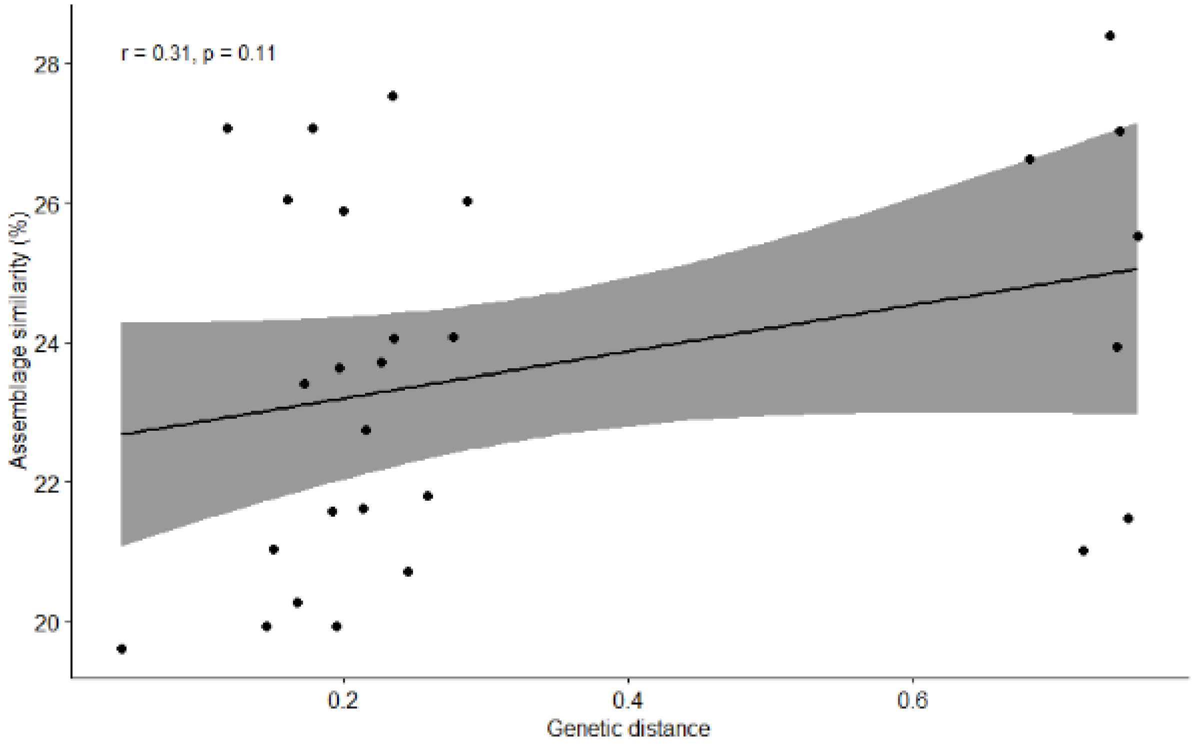

Figure 8: Scatterplot indicating the relationship between genetic distances of host trees with percentage similarity of beetle assemblages with spearman rank correlation coefficient reported.

Cunonia capensis has 25 congeneric species on the island of New Caledonia (Pillon et al. 2008). This genus has an interesting global distribution, as no species occurs on other southern land-masses with a Gondwanan linkage, i.e. Australia, New-Zealand or southern South America. A total of 87 beetle species and 564 individuals were sampled from this tree species (Supplementary material, Tables S4 & S5), comprising 27 families. The most abundant family was Chrysomelidae. The species, *C. capensis*, did have one beetle species preferring its leaf crown (Chrysomelidae: morpho-code C38), part of a family well-represented on the island of New-Caledonia (Jolivet & Verma 2008), where it has relatively high levels of endemism. The beetle species C38 comprised, on average, 10.5 ± 4.4 individuals per sampled *C. capensis* tree, compared to the next highest, *O. ventosa* with only 2.1 ± 1.2 individuals per tree. Chrysomelidae has a global distribution, making conclusions on the pre-Gondawan relationship between this species and its tree host not possible (Jolivet & Verma 2008). However, more work on the genus *Cunonia* and its associated insect herbivores from New Caledonia could shed light on this. Interestingly, the beetle family Chrysomelidae was relatively abundant in canopies of *C. capensis*, outnumbering the Curculionidae, a pattern not found in any other tree species here (Supplementary material, Table S4). Also, *C. capensis* had the largest diversity of a rare beetle family, Byrrhidae, consisting of three species and 12 individuals (Supplementary material, Tables S4 & S5). This family is well-described from the northern hemisphere, but still poorly known from the southern hemisphere (Lawrence et al. 2013).

Lowest species richness was found in *P. trifoliatus* canopies (81), a Gondwanan relict tree in the tribe Schizomerieae, with its phylogenetically closest relative occurring on the island of Tasmania (Jud et al. 2018). The most species rich and abundant families for this species were Curculionidae and Chrysomelidae, contributing 11 species each. On Tasmania, canopies revealed the most species rich families to be Curculionidae (22 spp.) and Chrysomelidae (14 spp.) (Keble Williams 2012). These were also the same two species-rich families, in the same order, from a subtropical forest in Australia (Basset 1992). Arguably, interactions between canopy beetles and specific tree species can be maintained over paleo-historical timelines. The family Carabidae (9 spp.) was also relatively well represented in *P. trifoliatus* canopies. Another family, Silvaniidae, was only sampled from *P. trifoliatus* canopies.

From southern Chile, *Podocarpus nubigena* were fogged together with *Laurelia sempervirens*, from which 140 beetle species from two different areas were found (Arias et al. 2008). We sampled a total of 97 beetle species from 15 individuals of *P. latifolius* here. From the Chilean fogging study, combining tree species from the genera *Nothofagus*, *Laurelia*, *Podocarpus* and *Araucaria*, the superfamily Curculionoidea was the most species rich (19% of total richness), followed by Tenebrionoidea (18%) and Staphylinoidea (16%). Here, for *P. latifolius* only, the most species rich families, as expressed in percentages, were Curculionidae (13.4%), Chrysomelidae (10.3%) and Staphylinidae (9.3%), with Tenebrionidae only comprising 3.1% of total richness for this tree species. However, interestingly *P. latifolius* was the tree species with the highest abundance of tenebrionid beetles sampled (22 individuals), followed by the next highest, *O. ventosa*, (12), and *R. melanophloeos*, (4). Therefore, although being a species-poor family in these forests, tenebrionids seem to have a preference for *P. latifolius*, as indicated by their relative abundances. As mentioned, *P. latifolius*, together with *C. capensis*, hosted the most disparate assemblages of canopy beetle fauna.

Whereas Anthicidae is abundant in the tropics (Erwin & Scott 1980; Stork 1987), this was not the case for a subtropical tree near Brisbane, Australia (Basset 1991). Here, Anthicidae was the 3rd most abundant predator family, being most common in *O. ventosa* canopies. *Olinia ventosa*, part of a western Gondwanan clade (Schönenberger & Conti 2003), also supported highest beetle abundance (888 individuals), represented by 88 species. The weevils completely dominated samples for this tree species, with over half of the catch (55.74%) from this tree being curculionids. Despite this relatively high abundance, *O. ventosa* only had the second highest species richness of Curculionidae, together with *C. dentata* (15 spp. each). The family Colydiidae was poorly represented in this study, and only sampled twice, in Kleinbos and Grootvadersbosch, solely from *O. ventosa* canopies.

The species with the highest richness of Curculionidae, was *O. c. macrocarpa*. Eighteen species were sampled from its canopies. Three of these species were only found in canopies of *O. c. macrocarpa*, although two were singletons and one only found twice, indicating their rarity. Erwin (1983) concluded from Manaus, Central Amazonia, that the top five species rich families of beetle are Curculionidae, Chrysomelidae, Tenebrionidae, Coccinellidae and Cerambycidae in order from most species rich to least species rich. In Brunei, from five tree species, the most species rich beetle families were Curculionidae, Staphylinidae, Chrysomelidae, Aderidae and Anthribidae (Stork 1991). Another study, from the temperate rainforests in Chile which focused on Gondwanan lineages, found nearly 500 beetle species, the most abundant and species rich family being Curculionidae (Arias et al. 2008). Evidently, curculionids are a species-rich group in canopies from temperate and tropical areas, with the southern Cape being no exception. Why *O. c. macrocarpa* specifically hosts relatively more curculionid species richness, remains uncertain. This tree species does not form part of the Gondwanan lineages, as most other species here and sampled by Arias et al. (2008) do, and are found in the olive family. In terms of its morphology, the leaves of *O. c. macrocarpa* are very leathery, and its wood comparatively hard and dense, from where it derives its common name as Ironwood (Von Breitenbach 1974). Perhaps, the unique feeding mechanisms of curculionids, which have elongated snouts (Picker et al. 2004), allow them to exploit *O c. macrocarpa* as a resource. With a total beetle species richness of 104, *O. c. macrocarpa* also hosted the highest beetle richness. After the curculionids, the second most species-rich family for this tree species was Staphylinidae.

The tree species with the second highest beetle richness, was *C. dentata*, which is in a mono-specific family, Curtisiaceae, and has a disputed phylogeny. However, its hosted beetle fauna is mostly generalist in relation to the other tree species sampled. Although only one species in the family Ptiliidae was collected, most individuals of this minute species were sampled from *C. dentata* canopies. Ptiliidae has a cosmopolitan distribution (Darby 2013; Ghahari 2017; Darby 2019). New Zealand, for example, hosts about 56 species of Ptiliidae beetles (Johnson 1982). In southern Africa this family is poorly known (Scholtz & Holm 1985).

Two species of the family Languriidae were sampled, one of which was collected from a single *C. dentata* canopy, and the second species from *R. melanophloeos*. Together with *C. dentata*, the tree species *R. melanophloeos* also hosted the highest abundance of the family Corylophidae (14). However, these were all represented by a single species, compared to *C. dentata* which hosted four species, the highest richness of this family for any tree species sampled. The second lowest abundance of beetles was sampled from *R. melanophloeos*, with its generalist beetle assemblage. The species *P. tricuspidatus* similarly had a generalist beetle assemblage. However, the family Chrysomelidae was the most species rich in canopies of *P. tricuspidatus* (14 spp.).

Hymenopterans

Here, the Hymenoptera: Parasitica was the most speciose taxonomic group, with 472 species. From a subtropical forest tree in Australia, non-Formicidae Hymenoptera were poorly represented in fogging samples (Basset 1991). However, two studies in three areas which sampled canopy arthropods through fogging, also report the Hymenoptera: Parasitica to be the most speciose. This includes fogging of trees in temperate Britain and subtropical South Africa (Moran & Southwood 1982), as well as tropical Borneo (Stork 1988, 1991). Parasitoid wasps were also strikingly species rich from tree canopies in Sulawesi, Indonesia (Noyes 1989). Although the hymenopterans were only identified to order here, the family Ichneumonidae (Hymenoptera) has been proposed to be the largest animal family globally from a tropical forest study (Veijalainen et al. 2014), highlighting the diversity of wasps globally. Indeed, in a Borneon study, Stork (1991) reported 945 species of non-Formicidae hymenopterans, more species rich than beetles (859) and more than double the richness of the third most speciose group, the flies, at 444 species sampled. More recently, Forbes et al. (2018) suggested that hymenopterans, dominated by micro-parasitoid wasps, comprise the largest insect order, being more speciose than beetles. Our results therefore fits the global narrative in terms of exceptional non-formicid hymenopteran diversity, especially in forest canopies.

Reasons for the high diversity of hymenopterans in forest canopies remain speculative. From a broadleaf forest in Germany, parasitoid wasps were found to be highly specialized toward host species, indirectly linking the parasitoid assemblage to tree-level resources (Ebeling 2008; Sobek et al. 2009). This was also found for a web-spider parasitoid wasp in Czech Republic (Korenko et al. 2011a), with web-spiders known to have tree host preferences (Korenko et al. 2011b). Also, many species of hymenopterans are gall-formers, which would directly link this higher trophic level to species of tree, as many gall-forming wasps have host preferences (Ronquist & Liljeblad 2001). Furthermore, hymenopterans in forests actively differentiate between vertical strata to most effectively detect often specialized resources within a heterogeneous floral environment (Compton et al. 2000). Moreover, certain species flying above canopy height are largely active at night, compared to more diurnally active species in lower levels of the forest strata due to environmental constraints on flight success in different forest layers (Compton et al. 2000). Therefore, structurally complex and diverse environments of forests might indirectly drive hymenopteran diversification through niche specialization (Lassau & Hochuli 2005).

Flies

Flies were very diverse here, comprising 13.7% (n = 211) of all species and 12.7% (n = 2 642) of all individual specimens sampled. Indeed, in a review of canopy studies, Basset (2001) argues that flies are the second most abundant taxonomic group, after the ants, in forest canopies. This was also the case for a tropical fogging study in Borneo, with flies even outnumbering ants and being the third most speciose taxonomic group (Stork 1991). Also, from a canopy fogging study in Mexico, flies were second only to beetles in terms of their species richness, with a total of 144 species (Cruz-Angón et al. 2009). Despite high levels of diversity, which is further reaffirmed here, dipterans are often neglected in taxonomic studies, and their role in forest canopies is still poorly understood. As noted by Orford et al. (2015) and Ssymank et al. (2008), flies are critically important for the process of pollination. As pollinators, flies might contribute greatly to the reproduction fitness of various tree species. Also, some flies are predatory (i.e. Empididae, Tachinidae; Stork 1991), thereby shaping canopy assemblages, whereas flies termed ‘tourists’ might feed on extrafloral nectaries, honey dew or fungi on leaf surfaces (Stork 1991). Therefore, reporting on dipteran diversity in future canopy studies could provide valuable insights and allow comparisons between global forests, and even between species of tree (Chapter 4 of this thesis).

Spiders

I sampled a total of 2 388 individuals and 90 spider species in 28 families. From a Tanzanian montane forest, canopy fogging produced 149 spider species, also from 28 families (Sørensen 2003). From numerous forests across tropical Africa, one fogging study on 15 different tree species gave a total of 84 species from a single spider family, Linyphiidae (Seyfulina & De Bakker 2008). Interestingly, Linyphiidae was the most speciose family in temperate beech forests in central Europe, followed by Theridiidae (Hsieh & Linsenmair 2011; Table 6). A study in north temperate forests sampled a total of 80 spider species and 16 spider families using canopy fogging (Hsieh & Linsenmair 2011). From 175 trees fogged in lowland forests of Eastern Poland over three years, a total of 140 spider species were sampled (Mupepele et al. 2014). From only ten trees in tropical Brunei, fogging produced 190 spider species (Russell-Smith & Stork 1995). Evidently, we witness an increase in canopy spider diversity moving from temperate to tropical forests, although this might be driven by an increase in micro-habitats associated with increases in plant diversity, and may not reflect spider diversity relative to their surrounds (Mupepele et al. 2014).

The family Theridiidae has a worldwide distribution, and is one of the most diverse spider families with more than 2 300 species (Agnarsson 2004), being especially diverse in forest canopies (Table 6). From our results, the most speciose families were Theridiidae, the cobweb spiders, Araneidae, orb-weaver spiders, and Thomisidae, crab spiders, consisting of 13 species each (Table 6; supplementary material, Table S6). Together, these families represented 43% of all spider species. Theridiidae was the most speciose family from an African mountain forest canopy in Tanzania, and contributed 26% of spider species richness (Sørensen 2003) compared to 14% here. It was also the most speciose family from a tropical forest canopy in Brunei, where Theridiidae contributed 28.9% of spider species richness (Russell-Smith & Stork 1995). From the canopies of floodplain forests near Leipzig, Germany, Theridiidae was both the most speciose and abundant family (Otto & Floren 2010). From tree canopies in both tropical Amazonia and temperate Europe, this family was the second most species-rich spider family (Höfer et al. 1994; Hsieh & Linsenmair 2011). Theridiidae was the second most abundant family sampled here (after Clubionidae), followed by Thomisidae and Araneidae respectively. Also, Theridiidae was the most abundant family from an Australian subtropical forest canopy (Basset 1991) and a temperate European study (Hsieh & Linsenmair 2011). Evidently, the cobweb spiders, with their diverse morphology, ecology and behaviour (Agnarsson 2004), form an important role in forest canopies ranging from temperate to subtropical to tropical areas. Our findings therefore fit the global pattern in canopy spider diversity, in which Theridiidae is consistently one of the most diverse spider families (Table 6).

From the global patterns in spider diversity, despite being less diverse than the Theridiidae, Araneidae and Thomisidae form important components of canopy spider assemblages, although this differs greatly between regions. From a Tanzanian Mountain forest, neither Araneidae nor Thomisidae were in the top five most abundant families, but Araneidae was relatively high in species richness (Sørensen 2004). Similarly, from Indonesia, Araneidae was the third most species-rich family, and was also high in species richness in northern temperate forests (Otto & Floren 2007; Hsieh & Linsenmair 2011). Evidently, Araneidae seems to be relatively species rich in both tropical and temperate regions, including southern Afrotemperate forests studied here. Thomisidae seems less species rich in tropical canopy studies compared to more diverse families (Russell-Smith & Stork 1994; Sørensen 2004; Floren & Deeleman-Reinhold 2005), which also appears to be the case in temperate forest canopies (Hsieh & Linsenmair 2011). In this study, one species from the family Thomisidae, *Diaea dorsata*, is a non-native species originating from Eurasia. *Diaea dorsata* was relatively scarce here, compared to both other crab spiders sampled here and from a canopy study in its native range, where it is abundant (Otto & Floren 2007). Members of Thomisidae typically ambush their prey (Jennings 1974; Otto & Floren 2007), which might bring *Diaea dorsata* into direct competition for prey resources with native crab spiders, i.e. *Diaea puncta*, should its numbers increase over time. Indeed, cryptic invasions such as these might be occurring on a scale exceeding those of plant invasions (Papadopoulos et al. 2013; Foxcroft et al. 2017).

Here, the most abundant family was Clubionidae, or sac spiders, which was the second most abundant family reported from subtropical Australia (Basset 1991) and only the seventh most abundant family reported from Tanzania (Sørensen 2003). Clubionidae is a well-represented family from forest canopies in Sulawesi, Indonesia, where it prefers montane forests at ca. 1 150 m above sea-level (Russell-Smith & Stork 1994). Although seemingly less diverse and prominent than Theridiidae, this global family of spiders (Clubionidae) are generally well represented in forest canopies globally.

Table 6: Summary of the most diverse spider families from comparable canopy fogging studies across the globe for both abundance and species richness

Publication	**Höfer et al. 1994**	**Russell-Smith & Stork 1995**	**Sørensen 2003**	**Otto & Floren 2010**	**Hsieh & Linsenmair 2011**	**Basset 1991**	**Swart et al. (this study)**
Region	**Tropical**	**Tropical**	**Tropical**	**Temperate**	**Temperate**	**Subtropical**	**Temperate**
Most abundant spider families	Salticidae	Pholcidae	Linyphiidae	Theridiidae	Theridiidae	Theridiidae	Clubionidae
	Araneidae	Theridiidae	Oonopidae	Thomisidae	Araneidae	Clubionidae	Theridiidae
	Theridiidae	Clubionidae	Pholcidae	Linyphiidae	Anyphaenidae	Araneidae	Thomisidae
Most species rich spider families	Araneidae	Theridiidae	Theridiidae	Theridiidae	Linyphiidae	Theridiidae	Araneidae
	Theridiidae	Salticidae	Linyphiidae	Linyphiidae	Theridiidae	Araneidae	Theridiidae
	Salticidae	Araneidae	Salticidae	Araneidae	Araneidae	Salticidae	Thomisidae

The relatively high spider abundance (2388) and richness (90 spp.) compared to the ants (1178; 36 spp.) sampled here, might indicate that, similar to a rainforest tree from subtropical Australia, spiders have taken over some predatory roles from ants (Basset 1991; Katayama et al. 2015). Arguably, larger variation in climate in temperate areas favours spider functional diversity, compared to more climatically stable tropical regions (Platnick 1991; Cardoso et al. 2011). The high diversity of spiders in temperate areas might be further exacerbated by tree host-preference of canopy spiders, of which the underlying mechanisms remains poorly understood (Mupepele et al. 2014). In summary, the patterns in spider taxonomic diversity sampled from tree canopies here, show similarities to forests from tropical regions, i.e. tropical Africa (Sørensen 2003), but also include tropical regions in the Americas (Höfer et al. 1994) and even temperate Europe (Otto & Floren 2010; Hsieh & Linsenmair 2011).

Bugs

From tropical Borneo, hemipterans were the fourth most abundant and speciose group (Stork 1988). Here, the Hemiptera was more species rich than the spiders, being the fourth most speciose order after the Hymenoptera, Coleoptera and Diptera. We sampled 129 species of Hemiptera, totaling 2 166 specimens. The most abundant and species rich family was Cicadellidae, with 750 individuals from 40 species (Supplementary material, Table S7). The Cicadellidae are particularly diverse in the Neotropical and Ethiopian regions (Nielson & Knight 2000), as well as in the Amazonian rainforest canopies, leaf hoppers were similarly diverse (Dietrich & Rakitov 2002). Importantly, Cicadellidae is also very speciose in the fynbos vegetation, often surrounding Afrotemperate forests (Stiller 2002). Perhaps, the high number of species in the family Cicadellidae in Afrotemperate forests sampled here, indicates specialization and diversification with regards to tree species identity (Bennett & O'Grady 2012). Leaf hoppers are piercing/sucking herbivores, feeding largely on vascular fluids (Backus 1988). The great range of tree morphologies, phenologies, and physiologies in diverse forests might subsequently stimulate radiation of foliar herbivores, such as leaf hoppers (Bennett & O'Grady 2013).

Tingidae, Psyllidae and Rhyparochromidae were respectively the second, third and fourth most abundant hemipteran families here. Basset (1991) reported the most dominant hemipteran group to be

Psylloidea, followed by Cicadellidae, Achilidae, Flatidae and Issidae, from a subtropical rainforest tree in Australia. Here, the families Achilidae and Flatidae were comparatively rare, comprising just two individuals from one species, each (Supplementary material, Table S7). Overall, few canopy studies comprehensively report on the hemipteran diversity, despite it being an often speciose and abundant group, stretching across trophic guilds (Basset 2001).

Ants

The 36 species of ant sampled comprised 1178 specimens in five subfamilies (Supplementary material, Table S8), 5.7% of total abundances. Species estimates were 78.67 ± 33.24 (Chao2) and 64.68 (Jacknife2), which is relatively high compared to some other species estimates for tropical Africa, i.e. 52-58 (Yanoviak et al. 2008) and 57 (Fisher 2004). However, abundance of ants in canopies here compared to global patterns, but places southern Afrotemperate forests closer to temperate trees (0.2 – 3.0% of total abundances (Moran & Southwood 1982; Basset 1991). Tropical areas often support ant abundance that is much higher than this, such as canopy study from Borneo (33.7% of total catches; Dial et al. (2006)) and Central Amazonia (53.4% of total catches; Adis & Schubart (1984)). From tropical Africa, a total of 161 ant species were sampled from forest canopies (Schulz & Wagner 2002). However, in another tropical forest study from Cameroon, sampling from 167 large trees produced only 28 ant species (Dejean et al. 2000). The diversity reported in this study is higher than temperate forests of Central Europe, where fogging of 375 trees over two countries produced 12 ant species (Floren et al. 2014). Also, 17 ant species were sampled from canopies in Northern Bavaria (Dolek et al. 2009). In terms of richness, our study area therefore fits between northern temperate and Afrotropical regions, the latter showing much variation.

Here, the most abundant ant was a species in the genus *Monomorium* in the Myrmicinae (Table 7). This genus has a global distribution (Heterick 2006), and is a diverse genus with over 300 described species (Bolton 1995; Heterick 2001; Fernández et al. 2007). It is mostly an Old-World genus, and is particularly diverse in the Afrotropical region (Fernández et al. 2007). However, from tropical Cameroon, a fogging study produced 97 canopy ant species, with the most abundant species belonging to Dolichoderinae: *Technomyrmex*, with *Monomorium* poorly represented (Watt et al. 2002). *Monomorium* species were also poorly represented in tropical Ugandan forest canopies (Schulz & Wagner 2002). Conversely, another forest survey in tropical Kenya, not restricted to canopy fauna only, showed Myrmicinae (of which *Monomorium* is a part) to be the most speciose subfamily followed by Formicinae (Garcia et al. 2009), which is very similar to the findings reported here (Table 7). Interestingly, from canopies in eastern Australian forests ranging from south to north, the subfamilies Formicinae and Myrmicinae were also the most speciose (Majer et al. 2001; (Table 7). Based on the dominance of subfamilies, southern Afrotemperate ant assemblages show similarities to most other global studies (Table 7). However, the sheer expanse of regional gaps impedes confident comparisons, especially between genera, which reveals great diversity in forest canopies and few latitudinal patterns (Table 7). Large areas which might share paleo-historical similarities in tree lineages with southern Afrotemperate forests, for example Afromontane forest canopies along the Afromontane archipelago, remains undersampled in terms of ant diversity.

Table 7: Summary of the most diverse ant genera from comparable canopy fogging studies across the globe for both abundance and species richness

Publication	**Floren et al. 2014**	**Floren et al. 2014**	**Dolek et al. 2009**	**Watt et al. 2002**	**Majer et al. 2001**	**Majer et al. 2001**	**Majer et al. 2001**	**Swart et al. (this study)**
Region	**Tropical**	**Temperate**	**Temperate**	**Tropical**	**Temperate**	**Subtropical**	**Tropical**	**Temperate**
Most species rich ant genera	*Camponotus*	*Lasius*	*Formica*	*Crematogaster*	*Monomorium***	*Technomyrmex*	*Crematogaster*	*Plagiolepis*
	Polyrhachis	*Formica*	*Lasius*	*Cataulacus*	*Prolasius***	*Camponotus*	*Camponotus***	*Tetramorium*
	Echinpola	*Camponotus*	*Myrmica*	*Polyrhachis*	*Anonychomyrma*	*Myrmecorhynchus**	*Technomyrmex***	*Camponotus**
Most species rich ant subfamilies	Formicinae	Formicinae	Formicinae	Myrmicinae	Formicinae	Myrmicinae	Myrmicinae	Myrmicinae
	Myrmicinae	Myrmicinae	Myrmicinae	Formicinae	Dolichoderinae	Formicinae	Formicinae	Formicinae
	Dolichoderinae	Dolichoderinae	Dolichoderinae	Dolichoderinae	Myrmicinae	Dolichoderinae	Dolichoderinae	Dolichoderinae*

*Shared richness with other groups not listed

**Similar richness within region, listed alphabetically

In terms of the genera found, *Plagiolepis* was the most abundant ant genus. This genus naturally occurs in Africa, Eurasia and Australasia, containing roughly 100 species (Thurin et al. 2011). Moreover, *Plagiolepis* here was the most species rich genus, containing seven species. This genus was dominant in numbers, but not richness, from Sabah, Malaysia (Floren & Linsenmair 1998). Only one species of *Plagiolepis* was sampled from Eastern Australian forest canopies (Majer et al. 2001) and from Central African canopies (Yanoviak et al. 2008) respectively. Therefore, the high diversity of *Plagiolepis* seems to be unique to canopies of southern Afrotemperate forests. The second and third most abundant ant species were *Plagiolepis decora* and *P. brunni*. From a Kenyan tropical forest, *P. decora* was also sampled, indicating the wide range of certain ant species, linking southern Afrotemperate forests with forests of Guineo-Congolian origin (Garcia et al. 2009). Similarly, *P. brunni* transverses the continent (Madl 2019).

Other parts of the globe report differential patterns in the taxonomic representation of canopy ants. In Central Europe, for example, the genus *Lasius* are among the most abundant (Floren et al. 2014). A Malaysian canopy study revealed *Camponotus* and *Polyrhachis* (Floren et al. 2014) as the most species-rich genera. In Borneo, the most abundant genera were *Dolichoderus*, *Technomyrmex* and *Crematogaster* (Floren et al. 2014), with Stork (1991) reporting from the same region relatively high abundance in the genus *Crematogaster*. In terms of richness, from a tropical forest in southern Thailand, *Crematogaster* was the most species-rich genus (Jantarit et al. 2009). From a canopy fogging study in Malaysia, a total of 143 ant species were sampled, the most species rich genus being *Crematogaster* (Floren et al. 2002). The abundance of *Crematogaster* was also noted from tropical forest canopies in Cameroon (Dejean et al. 2000; Watt et al. 2002) and Uganda (Schulz & Wagner 2002). Here, *Crematogaster*, was only the third most abundant genus sampled after *Plagiolepis* and *Monomorium*. This was similar to findings from Eucalyptus canopies in semi-arid North-Western Australia, where the most abundant ant species were in the genera *Iridomyrmex*, *Monomorium* and *Crematogaster* (Andersen & Yen 1992).

Conclusion

Although this area is temperate, these forests have a tropical floristic affinity. Tree species diversity in these forests is relatively high, although the canopy arthropod diversity reported here is less than expected compared to other global canopy studies, perhaps due to forests being naturally composed of isolated patches. Despite this, species estimates, and the high number of undescribed species, justifies special conservation efforts to protect southern Afrotemperate forest canopies, especially as the canopy layer seems to support a disproportionately high number of arthropod species compared to the forest floor in this region (Swart et al. 2018). In terms of the beetle diversity sampled, I propose that southern Afrotemperate forests lies closer to temperate regions than to tropical regions. Species richness estimates for beetles are strikingly close to a Chilean temperate rainforest, in which Gondwanan tree elements were fogged similar to here. The most diverse beetle families sampled here were similarly well-represented in forest canopies ranging from temperate to tropical regions.

The weevils specifically, seem to be one of the most diverse insect families in forest canopies, here and globally. Similar to some other canopy studies and recent predictions (Forbes et al. 2018), the non-formicid hymenopterans here were more species rich than beetles. Also, southern Afrotemperate canopies host dominant arthropod groups that are similarly dominant in most other forest canopies across the globe, these being the flies, bugs, spiders and ants. Differences were evident between the selected host tree species for beetle assemblages.

As I only sampled from eight tree species in forests containing <47 canopy species, I strongly argue that the diversity reported here might be a severe underestimate of the true diversity within these forests. This is further confirmed by the species estimates, which neared 3 000 arthropod species from the current dataset. Losing one tree species will inevitably cause numerous local-scale extinctions, which will probably go unnoticed. This should encourage more documentation of forest arthropods in this region especially. Similarly, between the different forest patches in this study, I report differences in beetle assemblages, despite being all classified as southern Afrotemperate forests. Therefore, conserving these forests as individual entities within the landscape is important to avoid huge local extinctions in the canopy layer with the loss of single forest patches.

I conclude that southern Afrotemperate forests have less-than-anticipated arthropod diversity within its canopies when considering their tropical appearance and paleo-history, but yet well-placed in a temperate context. However, the diversity reported here is possibly more than ten-fold compared to forest floors in this same complex, and might represent only a fraction of the true diversity, therefore deserving more research and conservation efforts.

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Supplementary material

Text S1 - Tree species information:

Cunonia capensis (Cunoniaceae): The red alder is a large tree species, reaching heights of up to 25 m. It is typically found near forest edges, or wetter microsites within developed forest, i.e. next to water courses (Von Breitenbach 1985). It has relatively large opposite leaves, with leaflets stalked, between 60-120 mm long. The leaflets are broadly lanceolate, pointed and has serrated leaf margins. Red alder leaves are typically leathery, dark green and glossy. The species flower in autumn, between March-May, and were not flowering during canopy sampling (Venter 2011). *C. capensis* are distributed from the mountain forests of the Cape Peninsula, becoming especially abundant in the southern Cape forests, and is also found in KwaZulu-Natal and the north-eastern forests of South Africa. Only one other species on the subcontinent is also part of the family Cunoniaceae, *Platylophus trifoliatus*, which is also included in this study. Red alder's closest relatives, in the genus *Cunonia*, are only found on the island of New Caledonia, where 25 endemics occur naturally (Pillon et al. 2008). Evidently, this species has an ancestral link with Gondwanan flora.

Curtisia dentata (Curtisiaceae): The assegai is a medium-sized tree, reaching heights of up to 18 m. It forms a straight, cylindrical trunk with a dense canopy (Venter 2011). Its leaves are 60-120 mm long, broadly elliptic to ovate, with coarsely serrated margins. The leaves are leathery, dark green and glossy above. Inconspicuous flowers are produced from October-March (Von Breitenbach 1974). Selected trees were assessed for flowers before sampling, and specimens were chosen which did not have any visible flowers. *C. dentata* is found from the Cape Peninsula to Mozambique, and ranges from being a small tree in dry shrub forests, to a middle-sized canopy tree in high-forests. It is the only member in a monospecific family, Curtisiaceae, and was previously placed in the cosmopolitan dogwood family (Cornaceae). Its phylogeny is still disputed; however, in the southern Cape forests it is accepted to be phylogenetically isolated within its natural habitat with no close, or arguably even distant, relatives.

Olea capensis macrocarpa (Oleaceae): The ironwood is a large to very large canopy tree, obtaining heights of up to 35 m. Its trunk is typically straight and cylindrical. Ironwood leaves are leathery, dark green and has wavy margins, between 70-150 mm (Venter 2011). Flowering occurs between November-April, with numerous small, white flowers forming at the ends of branchlets (Von Breitenbach 1974). Selected trees were assessed for flowers before sampling, and specimens were chosen which did not have any visible flowers. *O. c. macrocarpa* occurs throughout forests, following the coast, from the Cape Peninsula to the Limpopo province. It is part of the olive family (Oleaceae), being closely related to other ironwood species from subtropical and tropical Africa, i.e. *O. chimanimani*, *O. hochstetteri* and *O. welwitschii* (Von Breitenbach 1974). In the study area, its closest relative is the subspecies *O. c. capensis*, which differs in its leaf morphology, size, fruit and preferred growing habitat from *O. c. macrocarpa*.

Olinia ventosa (Penaeaceae): The hard pear can reach heights of up to 25 m, forming large and spreading canopies. Leaves are dark green, with wavy margins, and reaches 40-80 mm in size. This species flowers between May-October (Venter 2011). It is found in forests and forest margins, restricted to the south-western and southern coastal forests of South Africa. Although the genus is viewed as a western Gondwanan clade, it is closely related to other species in this genus which are subtropical and tropical in their distribution, i.e. *O. radiata*, found in forests more eastward than the distribution of *O. ventosa*, and *O. emarginata*, which is found in the eastern and northern forests of South Africa and occurs in east African tropical forests. The family, Penaeaceae, also has numerous members, mostly shrubs and shrublets, in the neighbouring fynbos vegetation (Manning 2018).

Platylophus trifoliatus (Cunoniaceae): The white alder is a large, usually multi-stemmed tree reaching heights of up to 25m. It forms a wide, spreading canopy with leaves being trifoliate, 50-120mm long, with serrated margins and bright green colouration (Venter 2011). Small, white flowers are borne in December. *P. trifoliatus* has a limited distribution range, found in protected valleys from the Cape Peninsula to the southern Cape, only in forests or, more rarely, next to stream banks in the fynbos. It is the only species in its genus. Part of the Schizomerieae tribe in the Cunoniaceae family, this species' closest relative is on the island of Tasmania (Jud et al. 2018), indicating a Gondwanan origin.

Podocarpus latifolius (Podocarpaceae): The real yellowwood reaches heights of 25-33m, forming straight stems with laterally extending branches. Leaves of this gymnosperm are narrowly elliptic, with a glossy dark green and sometimes bluish colouration (Venter 2011). Individual leaves can be between 40-80mm in length, with mature leaves being thick and leathery. Being a dioecious species, male trees form cones (5-45mm) and female trees form fleshy receptacles (10mm), which bears the eventual seeds. These reproductive structures form between July-September (Von Breitenbach 1985). *P. latifolius* has an extensive distribution range, being found in evergreen mountain forests and coastal forests from the Cape Peninsula northwards into subtropical Africa. Its closest relative is *P. elongatus*, a smaller and shrubbier tree occurring in drier western mountain forests and river banks, and *P. henkelii*, which is found in eastern forests as a large forest tree. None of these species, however, co-occur with *P. latifolius* in the study area. Here, its closest relative, albeit distantly, is *Afrocarpus falcatus*, previously grouped in the genus Podocarpus. Members of the Podocarpaceae family are distributed across the globe, however show distinct patterns indicating a Gondwanan origin.

Pterocelastrus tricuspidatus (Celastraceae): The candlewood can reach heights of up to 20m tall, forming a straight stem with a dense crown. Leaves are dark green and shiny, with leaf margins rolled under, and typically between 50-80mm in length. Leaves are broad-elliptic and inversely egg-shaped. Small, creamy flowers are produced July-November (Venter 2011). It is found in forests and forest margins from the Cape Peninsula to the mountain forests of KwaZulu-Natal. Part of the Celastraceae family, one of the 10 largest tree families in Southern Africa, this species has numerous closely and distantly related species within its distribution range. The family has a distinct Gondwanan distribution. Within the study site, its closest relative is *P. rostratus*, which has reddish branchlets, grows at higher altitudes and has a different leaf morphology.

Rapanea melanophloeos (Myrsinaceae): The Cape-beech can reach heights of up to 25m tall, with straight stems forming a flat and dense crown in larger specimens. The leaves are leathery, dull and dark green above and typically clustered on the ends of branches. Leaves can grow large, between 70-140mm, with margins entire and rolled under. Flowers are borne between May-August (Von Breitenbach 1974). *R. melanophloeos* is found from the Cape Peninsula into tropical Africa, and in the study region forms a frequent canopy tree. The phylogeny of Cape-beech is disputed. The genus, *Rapanea*, has a global distribution, with species from Africa, India, Seychelles, Lord Howe Island and French Polynesia.

Table S2: List and details of global publications used to determine the relationship between latitude and beetle species richness per square metre of canopy fogged.

Region	Latitude*	Tree species	Tree individuals / replicates per sp.	Total beetle richness	Mean richness per tree	Sampling area (m²) per tree	Mean richness per 1m²	Study
Uganda	1	Numerous species (4)	64	1433		16	1,4	Wagner 2000
Sulawesi, Indonesia	1						1,22	Hammond 1997**
New Guinea	3	*Castanopsis acuminatissima*	8	418	117,88	13-23	3,32	Allison et al. 1997
New Guinea	3	*Lithocarpus celebicus*	2		89	13	6,85	Allison et al. 1993
Borneo	4	*Shorea johorensis*	4		176,74	20	8,84	Stork 1991
Borneo	4	*Shorea macrophylla*	2		143,5	20	7,18	Stork 1991
Borneo	4	*Pentaspadon motleyi*	2		71	20	3,55	Stork 1991
Borneo	4	*Castanopsis sp.*	1		103	20	5,15	Stork 1991
Venezuela	6						5,65	Davies et al. 1997**
Pantanal	16	*Vochysia divergens*	3	256		22-23	2,98	Marques et al. 2006
Australia	27	*Argyrodendron actinophyllum*	10	186		16.8	1,11	Basset 1991
South Africa	33	*Erythrina caffra*	3	58		5	3,87	Southwood et al. 1982
South Africa	33	*Quercus robur*	3	34		5	2,27	Southwood et al. 1982
South Africa	33	*Olea capensis macrocarpa*	15	104	15	9.47	1,58	Swart et al. (this study)
South Africa	33	*Curtisia dentata*	15	100	13,47	9.47	1,42	Swart et al. (this study)
South Africa	33	*Cunonia capensis*	15	87	12,47	9.47	1,32	Swart et al. (this study)
South Africa	33	*Olinia ventosa*	15	88	13,67	9.47	1,44	Swart et al. (this study)
South Africa	33	*Podocarpus latifolius*	15	97	13	9.47	1,37	Swart et al. (this study)

South Africa	33	*Pterocelastrus tricupidatus*	15	99	11,73	9.47	1,24	Swart et al. (this study)
South Africa	33	*Platylophus trifoliatus*	15	81	9,73	9.47	1,03	Swart et al. (this study)
South Africa	33	*Rapanea melanophloeos*	15	88	12,27	9.47	1,30	Swart et al. (this study)
Chile	37	*Araucaria araucana*	10	168	39,3	40	0,98	Arias et al. 2008
Chile	38	*Nothofagus dombeyi*	9	294	62,33	40	1,56	Arias et al. 2008
Ohio	39	*Acer saccharum*	6	66		4	2,75	Gering & Crist 2000
Ohio	39	*Fagus grandifolia*	6	47		4	1,96	Gering & Crist 2000
Ohio	39	*Quercus rubra*	6	60		4	2,5	Gering & Crist 2000
Ohio	39	*Quercus alba*	6	95		4	3,96	Gering & Crist 2000
Chile	39	*Nothofagus obliqua*	5	179	67,8	40	1,70	Arias et al. 2008
Britain	51	*Quercus robur*	3	53		5	3,53	Southwood et al. 1982

*Latitude were rounded off; in studies where tree individuals / replicates occurred over different latitudes, the median were used.

**Numbers obtained from Wagner 2000.

Table S3: Summary of the abundance and species richness of beetle families sampled from 5 southern Afrotemperate forests via canopy fogging over a west-east biogeographical gradient.

Family	Abundance					Species richness				
	OB	**GVB**	**KB**	**WV**	**WEB**	**OB**	**GVB**	**KB**	**WV**	**WEB**
Aderidae		1	2		4		1	2		2
Anobiidae	3	7	8	16	3	3	5	6	7	3
Anthicidae	26	49	49	47	107	4	4	6	5	4
Apionidae				1					1	
Bostrichidae	5	4	10	10	9	4	4	4	5	2
Brentidae	2					1				
Bruchidae	3	1			1	1	1			1
Buprestidae			1	1				1	1	
Byrrhidae	3	2	10	4	1	1	2	3	3	1
Cantharidae	1					1				
Carabidae	67	51	98	38	30	9	6	13	8	7
Cerambycidae	1	4	5	6	3	1	2	3	2	2
Chrysomelidae	34	203	211	90	119	10	5	13	11	12
Ciidae			1	1	1			1	1	1
Clambidae	13	40	26	20	49	3	2	4	2	6
Cleridae	4	13	17	18	4	4	7	7	4	3
Coccinellidae	35	15	119	71	52	7	4	11	11	10
Colydidae		1	1				1	1		
Corylophidae	2	5	11	18	28	1	1	3	4	3
Cryptophagidae	7	2	8	21	38	2	2	2	3	4
Cucujidae	4	9	2	13	6	3	4	2	6	5
Curculionidae	626	139	634	428	380	21	16	15	22	10
Discolomidae	1		1	2	2	1		1	2	1
Elateridae	5		4	24	2	1		1	2	2
Eucnemidae				1					1	
Hydrochidae		1					1			

Lampyridae			3	5	4			3	3	1
Languridae		1	1				1	1		
Lyctidae	2					1				
Meloidae	3			3		2			1	
Melyridae		5		1	4		2		1	1
Mordellidae	4	2		1		2	2		1	
Nitidulidae	16	9	15	15	4	4	4	5	4	3
Oedemeridae				30	2				1	1
Phalacridae		1	2	2	2		1	2	2	2
Ptiliidae	1	2			11	1	1			1
Ripiphoridae			1		1			1		1
Salpingidae	4	2		1	1	2	1		1	1
Scarabaeidae				5					2	
Scolytinae (sf)	2		1	2		1		1	2	
Scraptiidae	17	7	8	27	22	5	3	5	5	3
Scydmaenidae	1					1				
Silvaniidae	8	11	8	12	20	2	4	3	5	3
Staphylinidae	26	49	59	71	49	7	9	13	16	15
Tenebrionidae	35		4	1	5	4		1	1	2
Grand Total	961	636	1320	1006	964	110	96	134	146	113

OB = Oubos, GVB = Grootvadersbosch; KB = Kleinbos; WV = Woodville; WEB = Witelsbos. sf = subfamily.

Table S4: Summary of the abundance of beetle families sampled from different tree species via canopy fogging classified into feeding guilds

Guild	**Family**	**Overall**	***C. dentata***	***C. capensis***	***O. ventosa***	***O. c. macrocarpa***	***P. latifolius***	***P. tricuspidatus***	***R. melanophloeos***	***P. trifoliatus***
Detritivore	Cleridae	1				1				
	Cryptophagidae	76	7	22	8	11	2	6	11	9
	Eucnemidae	1						1		
	Hydrochidae	1								1
	Nitidulidae	59	8	7		2	10	6	4	22
	Ptiliidae	14	7	1	3		2		1	
	Tenebrionidae	45		3	12	1	22		4	3
Detritivore Total		197	22	33	23	15	36	13	20	35
Fungivore	Ciidae	3	1			2				
	Clambidae	148	20	8	35	21	16	21	24	3
	Colydiidae	2			2					
	Corylophidae	64	14	11	12	9	2	2	14	
	Silvaniidae	7								7
Fungivore Total		224	35	19	49	32	18	23	38	10
Herbivore	Aderidae	7	2	2		1		1	1	
	Anobiidae	37	6	5	7	6	3	6	3	1
	Apionidae	1			1					
	Bostrichidae	38	6	10	3	2	4	3	9	1
	Brentidae	2				2				
	Bruchidae	5	1				1			3
	Buprestidae	2						1	1	
	Byrrhidae	20	1	12		4	1		1	1
	Cerambycidae	19	5		3	3	3	3	1	1
	Chrysomelidae	657	87	196	73	57	64	53	56	71
	Cucujidae	34	15	5	2	1	3	5	1	2
	Curculionidae	2207	378	94	495	264	394	228	174	180
	Discolomidae	6	2			2	1	1		

	Elateridae	35	2	1	3	1	2	3	2	21
	Languriidae	2	1						1	
	Lyctidae	2								2
	Mordellidae	7	1	1		1	1			3
	Oedemeridae	32		32						
	Phalacridae	7			1	1	2		1	2
	Salpingidae	8		2	1			1		4
	Scarabaeidae	5		2		1		1	1	
	Scolytinae	5				1	2	1	1	
	Scraptiidae	81	12	4	15	12	16	7	11	4
	Silvaniidae	52	6	3	12	3	1	14	11	2
Herbivore Total		3271	525	369	616	362	498	328	275	298
Predator	Anthicidae	278	28	31	65	51	38	25	21	19
	Cantharidae	1								1
	Carabidae	284	27	28	47	72	26	18	31	35
	Cleridae	55	7	8	8	4	7	6	10	5
	Coccinellidae	292	35	37	28	35	56	28	30	43
	Lampyridae	12	1		2	2		3	2	2
	Meloidae	1		5					1	
	Melyridae	10	3	2	2	1	2			
	Ripiphoridae	2					1	1		
	Scydmaenidae	1	1							
	Staphylinidae	254	39	32	48	21	28	40	34	12
Predator Total		1195	141	143	200	186	158	121	129	117
Grand Total		4887	723	564	888	595	710	485	462	460

Table S5: Summary of the richness of beetle families sampled from different tree species via canopy fogging classified into feeding guilds

Guild	**Family**	**Overall**	***C. dentata***	***C. capensis***	***O. ventosa***	***O. c. macrocarpa***	***P. latifolius***	***P. tricuspidatus***	***R. melanophloeos***	***P. trifoliatus***
Detritivore	Cleridae	1				1				
	Cryptophagidae	7	2	4	2	3	1	3	1	1
	Eucnemidae	1						1		
	Hydrochidae	1								1
	Nitidulidae	11	4	1		1	7	4	3	4
	Ptiliidae	1	1	1	1		1		1	
	Tenebrionidae	7		1	2	1	3		1	3
Detritivore Total		29	7	7	5	6	12	8	6	9
Fungivore	Ciidae	3	1			2				
	Clambidae	7	1	3	1	3	3	2	4	1
	Colydiidae	1			1					
	Corylophidae	6	4	2	1	3	1	1	1	
	Silvaniidae	1		5			4			1
Fungivore Total		18	6			8		3	5	2
Herbivore	Aderidae	3	2	1	3	1		1	1	
	Anobiidae	18	4	3	5	5	3	3	3	1
	Apionidae	1			1					
	Bostrichidae	11	4	3	3	1	4	2	3	1
	Brentidae	1				1				
	Bruchidae	3	1				1			1
	Buprestidae	1						1	1	
	Byrrhidae	5	1	3		2	1		1	1
	Cerambycidae	5	2		2	3	2	3	1	1
	Chrysomelidae	30	8	8	11	8	10	14	7	11
	Cucujidae	11	6	3	2	1	2	4	1	1
	Curculionidae	46	14	15	15	18	13	14	14	11
	Discolomidae	3	1			2	1	1		
	Elateridae	3	1	1	1	1	1	3	1	2

	Languriidae	2	1						1	
	Lyctidae	1								1
	Mordellidae	4	1	1		1	1			1
	Oedemeridae	1		1						
	Phalacridae	5			1	1	2		1	2
	Salpingidae	4		1	1			1		2
	Scarabaeidae	2		1		1		1	1	
	Scolytinae	3				1	1	1	1	
	Scraptiidae	14	3	1	3	5	4	2	6	2
	Silvaniidae	10	2	1	3	2	1	4	2	1
Herbivore Total		187	51	43	48	54	47	55	45	39
Predator	Anthicidae	10	4	3	3	8	4	3	4	4
	Cantharidae	1			6					1
	Carabidae	26	8	5		6	5	9	6	9
	Cleridae	14	5	4	5	1	6	2	4	5
	Coccinellidae	21	7	7	5	8	7	6	5	7
	Lampyridae	5	1		1	1		2	2	1
	Meloidae	2		1					1	
	Melyridae	3	1	2	1	1	1			
	Ripiphoridae	1					1	1		
	Scydmaenidae	1	1							
	Staphylinidae	30	9	9	11	11	9	10	10	4
Predator Total		114	36	31	32	36	33	33	32	31
Grand Total		349	100	87	88	104	97	99	88	81

Table S6: Summary of the abundance of Araneae species sampled from southern Afrotemperate forest canopies divided into families. (F) = family.

Family	Species	Abundance	Abundance (F)
Amaurobiidae	*Chresiona convexa*	15	
	Chresiona sp.	12	
	Obatala armata	12	39
Anapidae	*Crozetulus rhodesiensis*	19	
	Crozetulus sp.	5	
	sp. 2	58	82
Araneidae	*Araneus holzapfelae*	1	
	Araneus sp.	23	
	Caerostris sexcuspidata	17	
	Cyclosa insulana	6	
	Cyphalonotus larvatus	2	
	Eriovixia excelsa	16	
	Eriovixia sp.	1	
	Gasteracantha sanguinolenta	8	
	Ideocaira triquetra	15	
	Larinioides sp.	5	
	Neoscona sp.	39	
	Neoscona subfusca	24	
	Prasonica sp.	30	187
Cheircanthiidae	*Cheiracanthium* sp.	10	10
Clubionidae	*Clubiona* sp. 1	858	
	Clubiona sp. 2	11	
	Clubiona sp. 3	2	
	Clubiona sp. 4	6	877
Deinopidae	*Menneus* sp.	8	8
Dictynidae	*Dictyna* sp.	2	
	Mashimo leleupi	11	13
Eresidae	*Gandanameno fumosa*	1	1
Eutichuridae	*Cheiramiona* sp.	2	2
Gnaphosidae	*Aphantaulax signicollis*	8	
	sp. 1	3	11
Hahniidae	*Hahnia* sp.	1	1
Hersiliidae	*Hersilia setifrons*	3	3
Linyphiidae	*Afribactrus stylifrons*	8	
	Mecynidis dentipalpis	11	
	Pelecopsis sp.	33	
	sp. 1	8	60
Mimetidae	*Ero capensis*	9	
	Mimetus sp.	10	19
Oonopidae	*Australoonops granulatus*	8	8
Oxyopidae	*Hamataliwa strandi*	3	3
Philodromidae	*Philodomus* sp. 1	4	4

Pholcidae	*Quamtana knysna*	17	17
Salticidae	*Myrmarachne* sp.	41	
	Thyene coccineovittata	90	131
Scytodidae	*Scytodes cedri*	65	
	Scytodes sp.	2	67
Tetragnathidae	*Leucauge argyrescens*	15	
	Leucauge decorata	42	
	Leucauge sp.	2	
	Tetragnatha ceylonica	1	60
Theridiidae	*Argyrodes convivans*	19	
	Argyrodes sp.	71	
	Episinus sp.	18	
	Latrodectus geometricus	4	
	Phoroncidia sp.	41	
	Phycosoma sp.	19	
	Platnickina mneon	1	
	sp. 1	1	
	Theridion purcelli	9	
	Theridion sp. 1	195	
	Theridion sp. 2	2	
	Theridion sp. 3	7	
	Theridula sp. 2	4	391
Theridiosomatidae	*Baalzebub* sp.	17	
	sp. 1	3	
	sp. 2	38	
	sp. 3	1	59
Thomisidae	*Diaea dorsata*	2	
	Diaea puncta	38	
	Oxytate leruthi	40	
	Phaenopoma nigropunctatum	9	
	Pherecydes n. sp.	16	
	Pherecydes sp. 1	1	
	Phrynarachne melloleitaoi	5	
	Simorcus capensis	1	
	Synema vallotoni	3	
	Thomisus scrupeus	1	
	Tmarus cameliformis	19	
	Tmarus cancellatus	92	
	Tmarus sp.	7	234
Trachelidae	*Afroceto martini*	3	
	Jocquestus capensis	7	
	Trachelas penicillus	48	
	Trachelas setosus	9	67
Trochanteriidae	*Platyoides* sp.	4	4
Uloboridae	*Miagrammopes* sp.	1	
	Uloborus sp.	7	
	Zosis geniculata	6	14

Zodariidae	*Chariobas cylindraceus*		6	6
Grand Total		90	2388	28

Table S7: Summary of the abundance of Hemiptera families sampled from southern Afrotemperate forest canopies

Family	**Abundance**	**Species richness**
Cicadellidae	750	40
Tingidae	409	2
Psyllidae	311	10
Rhyparochromidae	187	12
Fulgoridae	94	1
Cercopidae	65	5
Gengidae	63	6
Pyrrhocoridae	59	7
Pentatomidae	37	8
Emesinae	36	2
Lygaeidae	28	3
Notonectidae	23	1
Meenoplidae	22	3
Enicocephalidae	18	4
Aphrophoridae	17	3
Delphacidae	12	4
Dictyopharidae	7	2
Cixiidae	6	1
Coreidae	6	1
Ischnorhynchinae	4	1
Cicadidae	3	2
Achilidae	2	1
Coccidae	2	1
Flatidae	2	1
Asopinae	1	1
Berytidae	1	1
Nabidae	1	1
Grand Total	2166	129

Table S8: Summary of the abundance of Formicidae species sampled from southern Afrotemperate forest canopies divided into subfamilies. (SF) = subfamily.

Subfamily	**Species**	**Abundance**	**Abundance (SF)**
Dolichoderinae	*Axinidris lignicola*	53	
	Tapinoma sp. 1	5	58
Formicinae	*Plagiolepis decora*	249	
	Plagiolepis brunni	167	
	Plagiolepis deweti	72	
	Plagiolepis jouberti	27	
	Polyrhachis spinicola	18	
	Plagiolepis sp. 1	18	
	Camponotus maculatus	4	
	sp. 2	2	
	Plagiolepis sp. 2	1	
	Plagiolepis puncta	1	
	Camponotus werthi	1	
	Camponotus auropubens	1	561
Myrmicinae	*Monomorium* sp. 2	275	
	Crematogaster liengmei	63	
	Nesomyrmex denticulatus	50	
	Tetramorium grassi	42	
	Crematogaster peringueyi	21	
	Tetramorium cf pusillum	16	
	sp. 3	7	
	sp. 1	4	
	Tetramorium capense	2	
	Pheidole sp. 3	2	
	sp. 5	2	
	Tetramorium regulare	1	
	Tetramorium longoi	1	
	Pheidole sp. 2	1	
	Pheidole sp. 1	1	
	sp. 4	1	
	sp. 2	1	
	Monomorium sp. 1	1	491
Ponerinae	*Hyponera spei*	2	
	Hyponera austra	1	3
Pseudomyrmicinae	*Tetraponera emeryi*	64	
	Tetraponera natalensis	1	65
Total	36	1178	5

Chapter 6 – General discussion and conclusions

With the explosion of angiosperms, today comprising ca. 250 000 species, insects were provided with a plethora of micro-habitats to exploit (Labandeira et al. 1994; Price 2002). This was done to great success, with plant-phytophage interaction webs, for example, comprising more than 40% of extant biodiversity (Price 2002). Much of this is associated with forests trees and global biodiversity, as a result, is disproportionately weighed towards forest tree-arthropod interactions. These interactions often form central pillars in in forest ecosystems, in which biodiversity ranging from bacteria, fungi, lichens, mosses, amphibians, reptiles, birds and mammals are impacted. As ecologists, studying these interactions in ever increasing depth is necessary not only to ensure optimal biodiversity conservation, but also to understand threats to human societies that stem from the disruptions of these. The destruction of indigenous forests, globally, appears to be unstoppable. Rates of deforestation in the Brazilian Amazon, for example, have recently seen relative decreases in comparison to previous years, however, an area of ca 0.66 million hectares is still lost every year (Cerri et al. 2018).

In light of this I focused the current study on the plethora of arthropods and their multitude of different associations with forest trees. I set out to report on how tree-arthropod interactions can differ at various scales, including landscape-, plot-, tree species-, tree individual and physiological-levels, both for arthropods in tree canopies and arthropods associated with leaf litter of specific species of tree (Fig. 1). In the first chapter I provide a background to the current study, as a literature review of Afrotemperate forests and its affinities to other forests around the globe, and provide a research rationale for the current study. The second chapter focusess on the effect of the landscape that surrounds an individual tree on arthropod diversity in its canopy. I showed that both the context and contrast in which an individual tree is found can greatly impact the arthropods hosted in its canopy. The third chapter focusses on a key function provided by forest arthropods, decomposition. Here I showed that tree identity in forests are important for detritivorous arthropods on forest floors through species-specific leaf litter, explaining fairly high diversity of forest floor arthropods. In chapter four I showed that host tree species, plot characteristics (re: plot cover) and tree physiology affect associated canopy arthropod diversity in various and, sometimes, unpredictable ways. In the final chapter, I sketch an outline of the diversity of arthropods associated with southern Afrotemparate forest tree canopies for the first time, filling a substantial geographical gap in canopy science, whilst comparing this to other forests around the globe. In this concluding chapter, I would like to highlight the relevance of this study, and make recommendations for future research, by discussing each data chapter seperately.

The first data chapter (chapter 2) placed typically landscape-level parameters (context, contrast) on an individual tree species. From the current scientific literature, which reports great diversity of arthropods in tree canopies (not only restricted to herbivores feeding on leaves, encompassing various trophic levels), I made the prediction that individual tree canopies might be viewed, for the smaller biota at least, as habitat patches. If this would be the case, I argued, the parameters as set out by Wiens et al. (1993) might be equally applicable at the level of individual trees, measured in its canopy arthropod diversity. From the results reported here, it appears that typical landscape-level parameters can be applied to individual trees, with both tree context and contrast revealing effects on canopy arthropods. Tree context also impacted on tree physiology, an important consideration when studying arthropod diversity.

The results reported in chapter 2 has great consequences for biodiversity conservation, especially in urban and urban fringe areas, which continue to expand at the expense of natural landscapes. Promotion of nature conservation within cities might still be in an early phase, however, already transformed areas could be crucial in the long-term sustainability of many species, and humanity. With the current loss of insect diversity globally (Habel et al. 2019), even in natural areas (Hallmann et al. 2017), our focus must shift to also include urban areas. It is known that urban trees provide cooler inner-cities, and helps with air quality (Akbari et al. 2001), benefitting humans. Their aesthetic value further contributes to continual planting in cities (Sæbø et al. 2003). However, planting of trees in transformed areas, especially native species, provide a rare opportunity to offer alternative habitat for a myriad of tree-associated biota, such as arthropods, contributing to local biodiversity conservation. Importantly, I showed that native tree species in transformed settings may fail to host equivalent levels of arthropod biodiversity in its canopies compared to when these same trees grow in natural areas. To optimally conserve local arthropod fauna associated with indigenous trees, merely planting such trees is therefore not adequate. In fact, I would argue that it is equally important to consider a tree's surrounds as the species being planted, and so far as possible mimic the natural surrounds of trees in transformed contexts. Urban ecological networks could help much in this regard, where natural tree recruitment and succession can be promoted. Rivers through towns and cities provide an opportunity to promote such ecological networks, with many rivers originating in natural landscapes before entering populated areas (Gurnell et al. 2007). Property owners could be made aware of the natural vegetation type in which their property is located, and design gardens accordingly. For this, local nature conservation authorities should be equipped to advise the public on which plants are best to plant in specific areas, and in which type of contrasting plants, to promote conservation in urban areas. Again, this will require a mind-shift, not necessarily away from "the destruction of the Amazon and climate change", but to, on top of that, include our daily living environments in conservation planning. Indeed, the room in which I sit writing this, once was a natural area.

I have to acknowledge, however, that I only used one tree species to reach the conclusions in chapter 2. As such, I want to urge future work on this topic to include more than one species of tree, and more replicates, although I do concede that the sorting of canopy samples is very time-consuming. Canopy fogging is, however, not the only way to sample arthropods associated with trees, and similar aspects as the current study have been succuessfully studied using other sampling tecchniques (Le Roux et al. 2018).

The species studied here, *Podocarpus elongatus*, can largely be described as a forest tree, despite also being found on rock screes and open areas. Its natural contrast, therefore, tend to be low, mostly being surrounded by similarly high and dense vegetation. Other tree species, such as those found on savanna plains for example, might be optimally planted in higher contrast settings. Such considerations are important in city planning, and researchers / planners / managers should be aware of these before investing in urban ecological networks. The best way, perhaps, to conclude this chapter is to ask city planners, and property owners, to carefully study each tree species in question, within its natural context / contrast, and mimic its species-specific habitat requirements in transformed areas if possible.

The next data chapter focused on tree species-level, and how it might affect one of the most important processes in forests, namely decomposition. Similar to the previous data chapter, the idea for this work sprouted from viewing trees as habitat patches, here within a single forest, and within leaf litter, not canopies. The concept of home-field advantage (HFA) has been applied throughout the world, but never has it been applied to assess its applicability in single forests, between tree species, and how detritivorous arthropods might be involved in this phenomenon. I combined aspects of HFA theory with aspects of forest functioning, i.e. different species of tree having different rates of litter fall, leaf build-up beneath source trees due to limited senescent leaf dispersal in closed canopy forests and, although not directly tested in this chapter, differences in nutrients of leaf litter between different tree species. Arguably, this creates a heterogeneous forest floor, which, similar to the forest canopy, might drive adaptation and speciation of forest floor detritivores.

Here, I showed that the heterogeneity associated with forest floors, should be considered in conservation planning. Different tree species revealed differences in detritivorous arthropod diversity. I assessed only 3 species of forest tree, of which only one revealed arthropod responses towards tree-level HFA. Although limited evidence for decomposition HFA was detected, litter arthropods did seem to be greatly affected by identity of source trees. I therefore can not exclude the possibility that only certain species within forests might reveal HFA at the tree-level, or that temporal variation also plays a role. However, it is clear that losses of single species, or significant changes in tree assemblages in natural forests, would affect associated arthropods, even those in the detrital food web. This will have cascading effects on normal functioning of forest ecosystems, not only causing local extinctions of detritivorous arthropods, but ultimately, affect the important process of decomposition in forests. Natural tree species diversity should therefore be maintained and promoted, not only to conserve the biota associated with its foliage, branches and stems, but also to conserve the plethora of biota in the detrital food web dependent on certain species of tree. This theme is intruiging, and it is my hope that future research will be conducted to answer the many questions that were raised from work conducted in this chapter. Some of these include: 1) is HFA prevelant only for certain tree species in forests, and why, 2) what is the effect of rare vs. common tree species in this phenomenon, 3) to what extent are detritivorous arthropods able to detect species-specific leaf litter, 4) are there temporal variation in HFA, and if so, how does the nutrient balance over different seasons affect it and 5) are detritivorous arthropods able to shift between species-specific leaf litter with temporal nutrient variation between different source tree species?

The results pertaining to the effects of tree species identity on arthropods on the forest floor were largely echoed in the forest canopies, which formed the 4th chapter. I demonstrated to what extent tree species identity, plot characteristics and plant physiology can affect canopy arthropod diversity, and results indicated that the loss of even a single tree species will have significant effects on canopy arthropod diversity. Indeed, in mixed-species, diverse forests such as southern Afrotemperate forests, each species' canopy might be viewed, again, as habitat patches in their own right. Specialized arthropods in tree canopies therefore need to be able to detect their host trees successfully, and be able to migrate at certain times between individuals of the same species for reproductive and feeding purposes. Viewing forests in this light, might help better shape future management plans, which then need to take into account aspects regarding insect dispersal and tree recruitment.

Moreover, not only the species identity of trees, but also aspects regarding the plot cover surrounding trees, affected arthropod diversity patterns. This important result underlies a greater hypothesis: natural forest crown heterogeneity is essential to conserve differentially specialized arthropod assemblages, interconnected with species of tree. Relating back to chapter 2; planting of vast areas of single tree species will not necessarily conserve the plethora of arthropods associated with that specific species, due to the general complexities of indigenous forest crown layers, the context in which an individual tree is found and the contrast with neighbouring vegetation. A single species of tree might have vastly different physiologies depending on where it is found within a complex forest ecosystem. This might depend on the availability of light, or even distance to forest streams, or forest edges. Certain specialized canopy arthropods might prefer more light-exposed trees, whereas other species might be photo-negative, preferring climax vegetation, or lower layers of tree crowns. It is this complexity that comes to the forefront in chapter 4, reminding us that the interaction between forest trees and arthropods are much more complex than just host specificity.

Homogenized forest canopies, typically the case in plantations forests, may fail to conserve even ‘natural’ arthropods associated with the planted tree species, due to structural homogenization negatively affecting certain arthropod species, or altered tree physiologies stemming from greatly altered tree contexts. Again, the same can be said for indigenous trees planted in urban or suburban areas. Not only structural variation is important, though. I also show in chapter 4 that plant physiology is of great importance for canopy arthropod responses, but that these responses are extremely difficult to predict. Indeed, arthropod responses to tree physiology depended largely on tree species, with different species impacting associated arthropods differentially. The impacts of increased air pollution, changes in global temperatures and rainfall shortages causing drought, as examples, might all interact in complex feedback loops to create unpredictable arthropod responses. As such, I urge canopy scientists to include predictions of climate change, and climate variability, in future research where possible.

In the final chapter I aimed to place the canopy arthropod diversity of southern Afrotemperate forests in a global context, highlighting the uniqueness of forest canopies in the current study region. Here, numerous undescribed species were collected, contributing to future management strategies and conservation planning. We can now confidently deduce that non-formicid hymenopterans are the most speciose group in southern Afrotemperate forest canopies, followed by beetles. Also, from a global biodiversity perspective, southern Afrotemperate forests are closer to temperate- than to tropical forests in terms of canopy arthropod diversity. This baseline data will hopefully lead to more research into this relatively new frontier in this region, and I would like to urge local conservation authorities to continue to support research in this field. Throughout the current project, I became acutely aware of the large geographical gaps in canopy science. Although I understand the need to carry out long-term research on forest canopies, justified through the Canopy Crane Network which sees permanent canopy access facilities around the globe, I also want to urge researchers to expand this network, perhaps by starting research partnerships in areas of possible great importance in the field of canopy science. Given the large expanses of unexplored regions, many, and perhaps most, secrets are still to be uncovered in this last biotic frontier.

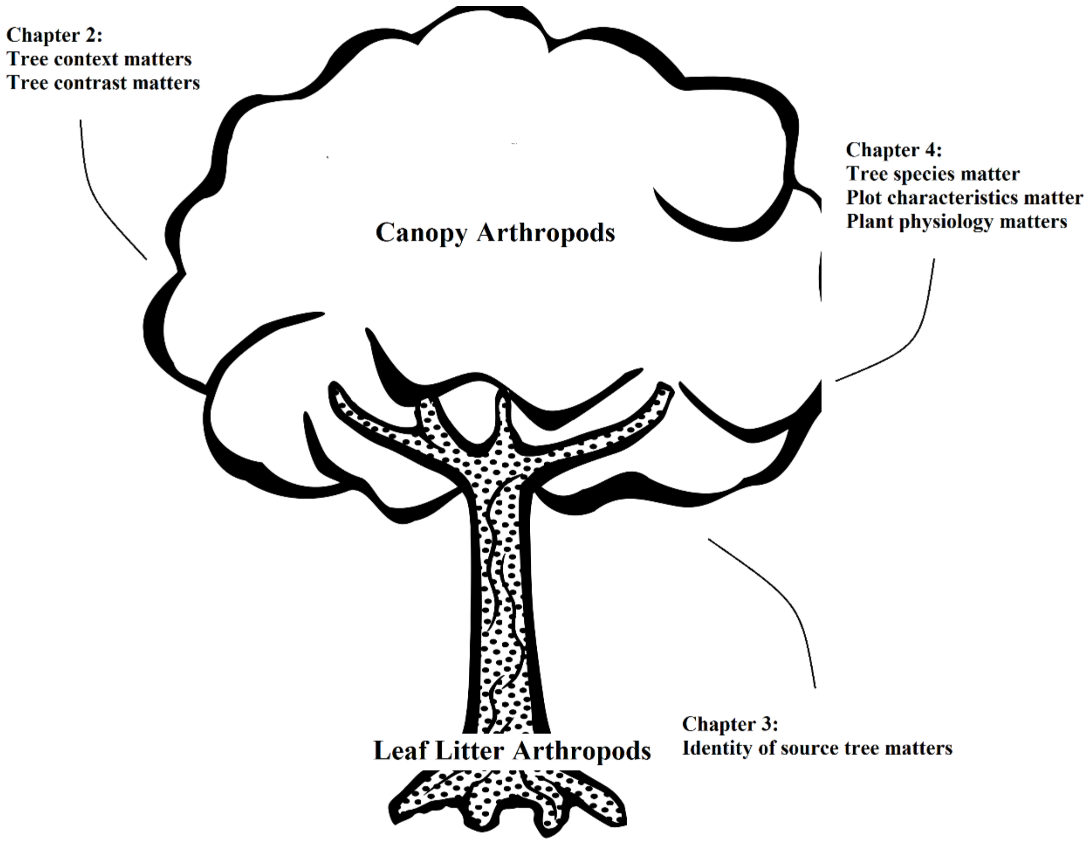

Figure 6: Illustrative summary of the main findings of this study relating to tree-arthropod interactions. Conserving a tree species' associated arthropods can be done within transformed areas if a tree's natural context and contrast is considered (chapter 2), and in natural forests, canopy arthropod diversity might respond to species identity, plot cover and plant physiology (chapter 4). Leaf litter arthropods, too, are affected by source tree species identity (chapter 3).

In conclusion, the current body of work highlights the importance of trees, as habitat patches, in conserving many other associated biodiversity. I argue that trees be viewed as habitat patches in their own right. The most important aspect from this thesis is that, although trees host disproportionate amounts of biodiversity, many factors contribute to the ability of trees to host associated arthropods.

Ecologists, conservation officers and managers need to be aware of these factors, and incorporate strategies to optimize the conservation potential of individual trees. Certain factors are directly associated with land-use strategies, such as promoting a natural tree context, or the planting of mixed-species plantations. Other factors are more subtle, such as those stemming from pollution, increased temperatures, higher incidence of drought and climate change, which will not only directly affect insects associated with trees, but also indirectly, through the altering of tree physiology. Mitigation strategies for such subtle changes are important, as well as more research. Should we lose the integrity of the last biotic frontier, the consequences for global biodiversity will without a doubt be severely felt.

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