

**THE IMPACT OF PINE PLANTATIONS AND  
ALIEN INVERTEBRATES ON NATIVE FOREST  
AND FYNBOS INVERTEBRATE COMMUNITIES IN  
TABLE MOUNTAIN NATIONAL PARK**

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**The impact of pine plantations and alien invertebrates on native forest and fynbos  
invertebrate communities in Table Mountain National Park**

Charmaine Uys (February 2012)

**ABSTRACT**

While the Cape Peninsula (South Africa) is renowned for its exceptional plant and invertebrate diversity and endemism, extensive alien plant invasions and exotic pine plantations threaten and reduce native species richness. This study frames invasion ecology theory in a conservation context, and examines the impact of planting and felling pine on litter invertebrate communities, by comparing invertebrate diversity between pine plantations and native vegetation. Impacts of the worst invasive alien invertebrate (Argentine ant, *Linepithema humile*) and other alien invertebrate species are investigated. This is one of the first attempts to inventory and quantify impacts of non-ant alien invertebrates in Table Mountain National Park. The entire ground-dwelling invertebrate community was sampled at 31 sites in summer 2008/2009, using soil cores, leaf litter samples, pitfall traps, sugar-baited ant traps and decayed logs. A total of 112 404 individuals, representing 728 species (10 classes and 38 orders), including nine Cape Peninsula endemic and 19 alien species, was collected. Pine plantations supported lower species richness and abundance, and different community assemblages, compared to Afrotropical forest, but similar species richness to fynbos. This supports previous local studies and global trends. Pine plantations shared fewer species with fynbos than forest, and negatively affect fynbos-specialist invertebrates, because afforestation reduced available fynbos habitat. Alien species richness was similar across habitats. Argentine ants, like most other alien species identified, were present in all habitats. The impact of Argentine ant invasion on native ant communities was evaluated using species richness and community composition analyses, species co-occurrence patterns (*C*-score), and the functional group approach. The comparative approach adopted provided no evidence for displacement, impoverishment, or community disassembly. No clear impacts of the 18 non-ant alien species on the abundance, species richness, or community composition of corresponding native taxa were detected. Disturbance history offers a more parsimonious explanation for the trends observed, particularly in fynbos. However, carnivorous molluscs require careful monitoring, given their abundance and known impacts elsewhere. Using a reiterative process and *IndVal*, two ant species (*Pheidole capensis* and *Camponotus bertolini*) were selected as ecological indicators of restoration progress in fynbos following clear-felling of pine. Ants similarly have application for monitoring in other Mediterranean-type ecosystems impacted by invasive pines.

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## CHAPTER 1. INTRODUCTION

### Setting the scene

Invasive alien species are the second leading cause of global biodiversity loss (Wilcove *et al.*, 1998; Simberloff, 2001), and interact additively or synergistically with the most important driver of loss, habitat destruction (Didham *et al.*, 2005). Alien species are those that did not originate from a geographic region in question (Richardson *et al.*, 2000; Pyšek *et al.*, 2004). Alien species span a naturalisation-invasion continuum (reviewed in Pyšek & Richardson, 2010), and become invasive when they spread widely in the newly occupied region (Kolar & Lodge, 2001). As such, biological invasions are recognised as global drivers of environmental change (Millennium Ecosystem Assessment, 2005). Biological invasions are on par with climate change as one of the hottest contemporary research topics within ecology, with a recent exponential increase in interest in the discipline of invasion ecology, to match the escalating global biological invasion crisis (Pyšek *et al.*, 2006; Richardson & Pyšek, 2008; Davis, 2009).

It is the accelerated rate of human-mediated spread, distances traversed and numbers of species involved that set current biological invasions apart from natural long-distance colonisations and range expansions (Cassey *et al.*, 2005). Consequently, many landscapes and seascapes in various parts of the world are now dominated by alien species (Cassey *et al.*, 2005; Didham *et al.*, 2005). Coastal ecosystems, inland waters, islands and Mediterranean-climate regions are most threatened by biological invasions (Pyšek & Richardson, 2010). This thesis will focus on biological invasions in the Mediterranean-climate region of the Western Cape Province, South Africa, and more specifically on the ecological impacts of terrestrial biological invasions.

The impacts of alien species on native biota are of particular concern, and have received a great deal of attention from researchers (Richardson, 2006). An impact may be defined as 'the description or quantification of how an alien species affects other organisms and the environment' (Pyšek & Richardson, 2010). Invasive alien species can displace native species, reduce their abundance, rapidly disassemble communities, alter community organisation and disrupt ecosystems (Vitousek *et al.*, 1996; Mack *et al.*, 2000; O'Dowd *et al.*, 2003; Sanders *et al.*, 2003; Blackburn *et al.*, 2004; Gaertner *et al.*, 2009). Impacts of the vast majority of alien species have not been quantified (Parker *et al.*, 1999), although most are assumed to have some ecological impact on the invaded ecosystem (Ricciardi & Kipp, 2008). Most such impacts are observed at the population or community level, but some invasive alien species also cause



impacts at an ecosystem level (Parker *et al.*, 1999; Pyšek & Richardson, 2010), where they disrupt major trophic networks and other ecological processes. The focus of this thesis is on population and community level ecological impacts on terrestrial invertebrates, resulting from pine invasions.

## **Ecological impacts of pine invasions in South Africa**

South Africa is well advanced in the field of biological invasion, certainly in comparison with the rest of Africa, because it has robust national legislation for tackling the biological invasion problem, and a relatively well-developed research information infrastructure (McGeoch *et al.*, 2010). South Africa accounts for roughly two-thirds of all published research on biological invasions produced on the African continent (Pyšek *et al.*, 2008). The country has a long history of research on plant invasions (reviewed in Chown, 2010), and is a global leader in the application of pine invasion research (Richardson, 2006). Unfortunately, South Africa also has one of the highest levels of alien plant invasion, compared to other countries (Richardson & van Wilgen, 2004).

Invasive alien trees have major impacts on native species richness. Pines (*Pinus* species) and Australian wattles (*Acacia* species) are among the alien invasive plants that cause the most significant declines in native species richness in South Africa (Richardson & van Wilgen, 2004; Gaertner *et al.*, 2009). These species are particularly problematic in fynbos, the Mediterranean-climate shrubland concentrated mostly in the Western Cape Province. Here dense stands of pines and wattles are known to reduce native plant diversity and abundance at small spatial scales (Richardson *et al.*, 1989). The Fynbos Biome is the most heavily invaded and best-studied of South Africa's eight terrestrial biomes (Richardson & van Wilgen, 2004), and also that which supports the highest proportion of endemic plant species. Given the severe impacts of pine invasions, especially in fynbos, this thesis is set in the Fynbos and Forest Biomes, South Africa's smallest and most heavily invaded biomes (Henderson, 1998). At least 21 *Pinus* species have become invasive, with severe impacts in South Africa and other Southern Hemisphere countries (Richardson *et al.*, 1994; Richardson, 2006). Pines represent a model taxon for studies on alien plant invasions, and many of the important insights gained from pine invasion studies are also relevant for other plant taxa (Richardson, 2006).

Most invasive pine species in South Africa are also commercially important forestry species (Richardson, 2006). Over 80 species of *Pinus* have been introduced to South Africa, seven of which now form the backbone of commercial forestry industries in the Southern

Hemisphere (reviewed in Richardson *et al.*, 1994). Pine plantations (the main focus of this study) are regularly spaced monocultures (Hartley, 2002). Although plantations are sometimes referred to as 'plantation forests' or 'pine forests', to avoid confusion the term "forest" is used here to refer only to native (indigenous) forest, and not also to planted or invasive stands of pine trees. Afforestation, the planting of large numbers of trees on previously non-forested land, is equivalent to a dense invasion. Therefore, studies of the effects of plantation forestry offer insights into the impacts of invasive alien trees. Afforestation has striking impacts on biodiversity in certain parts of South Africa, and has resulted in numerous plant and animal species becoming threatened, or being forced to local extinction (Armstrong *et al.*, 1998).

### **Ecological impacts of invertebrate invasions in South Africa**

Biological invasions by alien animals in South Africa have received far less attention than those by alien plants (Chown, 2010). The most comprehensive current list for South Africa cites 601 alien animal species (Picker & Griffiths, 2011), but is most certainly an underestimate, especially for invertebrates. Despite the large number of alien animal species (spanning most major taxonomic groups) in South Africa (Macdonald *et al.*, 2003; Musil & Macdonald, 2007), few have been well-studied. Consequently, most insights on the mechanisms and impacts of invasion come from studies of a few of the most harmful invasive alien species (Pyšek *et al.*, 2008).

Locally, the Argentine ant (*Linepithema humile*) has received more attention than most other alien invertebrate species, because its invasion into fynbos has caused the disruption and collapse of an ant-plant mutualism, namely myrmecochory, which involves the dispersal of seeds by ants (Bond & Slingsby, 1984). Argentine ants have also been reported to reduce ant species richness and to replace dominant native ants, in particular, ground-foraging, seed-dispersing ant guilds in fynbos (Bond & Slingsby, 1984; Parker-Allie *et al.*, 2008).

The Argentine ant and four other invasive ant species are listed among the *100 of the world's worst invasive species*, chosen for their serious impact on biodiversity and/or human activities, and their illustration of important issues surrounding biological invasion (Lowe *et al.*, 2000). Invasive ants are a globally pervasive ecological problem due to their expanding geographic ranges, high propagule pressure, high local abundances and ability to disrupt ecosystems (Holway *et al.*, 2002). High competitive ability, polygyny, dependent colony foundation and unicoloniality characterise these successful invasive ant species (Suarez *et al.*, 2010). Throughout the world, invasive ants also readily spread from human-modified habitats into undisturbed natural areas, under suitable abiotic conditions (reviewed in Krushelnycky *et*

*al.*, 2010). Therefore, Argentine ants, like pine plantations, are a focus of this thesis, given the conservation concern associated with their invasion, both locally and globally.

Non-ant alien invertebrates may also impact native invertebrate diversity, either directly through predation and parasitism, or indirectly by disease transmission, disrupting mutualisms and through interference competition (Kenis *et al.*, 2009). Therefore, in addition to the impacts of Argentine ants, the ecological impacts of other alien invertebrates (particularly Mollusca) are investigated. This is one of the first attempts to inventory and quantify ecological impacts of non-ant terrestrial alien invertebrates on the Cape Peninsula, in the Western Cape Province.

### **Implications of felling pine for invertebrate communities**

It is not enough to know the ecological impacts of planted or invasive stands of pine, or which invertebrate species survive under pine plantations. There is also an urgent need to start documenting and understanding the community compositional changes that take place post-felling of pine, in order to inform responsible and appropriate management decisions. Clearing invasive alien trees has tangible conservation benefits. For example, three species of endemic South African dragonflies that were feared extinct, are now known from sites from which invasive alien trees have subsequently been removed (Samways *et al.*, 2005; Samways & Sharratt, 2009). However, little is known about the recovery of invertebrate communities after clear-felling of pine. This study is one of the first attempts to fill this gap, and to identify potentially suitable invertebrate taxa to use as ecological indicators of restoration progress in fynbos following clear-felling of pine.

### **Broad aims and objectives**

This study was undertaken on the Cape Peninsula in Table Mountain National Park (Cape Town), a World Heritage Site and global biodiversity hotspot in the Cape Floristic Region. Alien pine plantations on the Cape Peninsula replaced fynbos, but are thought to support lower invertebrate species richness and different community assemblages, compared to neighbouring native forest (*e.g.* Ratsirarson *et al.*, 2002; Raharinjanahary, 2007; Stephens & Wagner, 2007; Pryke & Samways, 2009b). The primary overall aim of this study is to assess the implications of planting and felling pine for ground-dwelling invertebrates. The secondary overall aim is to profile and investigate the impacts of all ground-dwelling alien invertebrate species, since this has not previously been attempted on the Cape Peninsula. This study is a conservation priority,

because the Cape Peninsula supports exceptional invertebrate endemism, and many of these species are ground-dwelling (Picker & Samways, 1996). In doing so, this study frames invasion ecology theory in a regional conservation context, but the findings also have application to other Mediterranean-type ecosystems impacted by invasive alien pines. The impacts of alien plantations and alien invertebrates are a globally relevant conservation concern, given that invasive alien species are considered the second biggest threat to global biodiversity (Wilcove *et al.*, 1998; Simberloff, 2001).

The broad objectives of this study are:

- 1) To determine the influence of exotic pine plantations on ground-dwelling invertebrate species richness and community composition (Chapter 3).
- 2) To investigate the impacts of Argentine ants on native ants and other ground-dwelling invertebrates, and to investigate the impacts of other (non-ant) alien invertebrate species on their corresponding native taxa (Chapter 4).
- 3) To identify and test potentially suitable ground-dwelling invertebrate taxa for use as ecological indicators of restoration progress in fynbos following clear-felling of pine plantations (Chapter 5).
- 4) To integrate the findings of this study, discuss their implications for invertebrate conservation and management, and propose future research (Chapter 6).

## CHAPTER 2. STUDY SITES AND SAMPLING METHODS

### Study area

#### *Cape Peninsula*

This study took place in Table Mountain National Park, which stretches from Signal Hill (33°55'4"S 18°24'10"E) to Cape Point (34°21'26"S 18°29'51"E) on the Cape Peninsula (area: 471 km<sup>2</sup>), in the south-western tip of the Cape Floristic Region, and surrounded by one of South Africa's fastest growing metropolises, greater Cape Town. The Cape Peninsula forms part of the Cape Fold Mountains, and is renowned for its topographical heterogeneity (Cowling *et al.*, 1996) and exceptional biological diversity and endemism, with 158 endemic angiosperms (Helme & Trinder-Smith, 2006) and at least 111 endemic invertebrates (Picker & Samways, 1996) known to be restricted to the Peninsula. Serious threats to Cape Peninsula biodiversity include land transformations, alien tree invasions and altered fire regimes (Richardson *et al.*, 1996).

#### *The Fynbos Biome, with a focus on Sandstone Fynbos and Granite Fynbos*

The Fynbos Biome is one of five geographically distinct areas that together constitute the global Mediterranean Biome, the others being the Mediterranean Basin, Californian Floristic Province, a small region in North Chile and two separate regions in Australia (Rebelo *et al.*, 2006). The Fynbos Biome is subdivided into three main vegetation units: fynbos, renosterveld and strandveld. The fynbos alone boasts some 7500 of the almost 9000 plant species found in the Cape Floristic Region, over 80% of which are endemic to the region (van Wyk & Smith, 2001).

Fynbos is characterised by nutrient-poor soils; hot, dry summers and cool, wet winters; recurrent fires at 5-50 year intervals; and complex plant-animal interactions, especially pollination and dispersal (Rebelo *et al.*, 2006). Fynbos is both fire-prone and fire-dependent, with summer and early autumn fires necessary to maintain diversity and ecosystem processes (Forsyth & Bridgett, 2004). The current fynbos vegetation classification follows the underlying geology (Rebelo *et al.*, 2006). Two of the fynbos vegetation groups found on the Cape Peninsula, namely Sandstone Fynbos and Granite Fynbos, were included in the experimental design of this study.

Sandstone Fynbos is the most extensive vegetation group within the Fynbos Biome, covering roughly one third (301 km<sup>2</sup>) of the biome on the Cape Peninsula. Peninsula Sandstone Fynbos (Rebelo *et al.*, 2006) was previously classified (among other names) as Mountain Fynbos (Low & Rebelo, 1996). It occurs on gentle to steep slopes (up to 1086 m a.s.l.) across

the 50 km length of the Cape Peninsula, on stony, often very sandy, acid lithosol soils derived from Ordovician sandstone of the Table Mountain Group, a subdivision within the Cape Supergroup rocks. Mean Annual Precipitation (MAP) ranges from 520-1690 mm, peaking from May to August. Vegetation comprises mainly proteoid, ericaceous and restioid fynbos, with some asteraceous fynbos. Comparatively little land transformation has taken place in the mountain habitat, affording Sandstone Fynbos the conservation status of 'Least Threatened'. Nevertheless, urban sprawl and alien plantations have transformed large parts of this vegetation group, and dense patches of woody invasives occur, despite a long history of conservation in the mountains.

Granite Fynbos covers only 2% of the Fynbos Biome. Peninsula Granite Fynbos (Rebello *et al.*, 2006) is found on gentle to steep lower slopes (up to 450 m a.s.l.), below the sandstone mountain slopes on the Cape Peninsula, almost entirely surrounding Table Mountain. Soils are deep loamy, sandy soils, derived from the Cape Granite Suite. Mean Annual Precipitation ranges from 590-1320 mm, peaking from May to August. This diverse vegetation group is dominated by asteraceous and proteoid fynbos. Peninsula Granite Fynbos is listed as 'Endangered'. Although it is conserved in Table Mountain National Park and Kirstenbosch National Botanical Garden, much of this fynbos is senescent and undergoing transformation into Afrotemperate forest, as a result of the fire-exclusion policies in Orange Kloof and Kirstenbosch, and a reluctance to use fire on green belts and on the urban fringe.

#### *The Forest Biome, with a focus on Southern Afrotemperate Forest*

Forest covers 32% of dry land globally, of which 17% is found on the African continent (Dajoz, 2000). Forest is the smallest biome in southern Africa (Rutherford & Westfall, 1994; Eeley *et al.*, 2001), covering less than 1% of the combined land area of South Africa, Lesotho and Swaziland (Midgley *et al.*, 1997; Rutherford, 1997; Rouget *et al.*, 2004; Berliner, 2005). In southern Africa, there are over 20 000 patches of forest, ranging in size from less than 1 ha to over 2000 ha, but 71% of the patches are less than 10 ha (Berliner, 2005). Forest patches have a naturally fragmented distribution, scattered along the eastern and southern mountain ranges and coastal lowlands of southern Africa. This 'forest archipelago' is embedded in a matrix of temperate biomes, including fynbos, grassland, succulent thicket and savanna (Mucina & Geldenhuys, 2006).

Despite their small size and fragmented distribution, South African forests are globally significant in terms of biodiversity. A comparison of the plant species richness relative to the total area of each biome in South Africa shows that the forest biome contains the highest

density of plant species: 3000 species in approximately 5052 km<sup>2</sup>, compared to the next highest, fynbos, with 7500 species in 76 744 km<sup>2</sup> (Berliner, 2005). Southern African temperate forests are also between three and seven times richer in tree species than other forested regions of the Southern Hemisphere, with the richness of South African tree genera and families being unparalleled (Cowling, 2002).

Afrotemperate forests in southern Africa form part of the global warm-temperate Forest Biome (Rutherford *et al.*, 2006). Afrotemperate forests were previously known locally as Afromontane forests (*sensu* White, 1978). They share affinities with the Afromontane Region throughout sub-Saharan Africa, which occurs as a series of isolated patches constituting the Afromontane regional centre of endemism (White, 1983). Although most Afromontane communities in the tropics occur above 2000 m, forest occurs almost at sea level on the moist, sheltered, eastern slopes of Table Mountain, where latitude “compensates” for altitude and the climate is influenced by the proximity to the Atlantic Ocean (Meadows & Linder, 1989).

Based on a biogeographic-floristic classification of South African indigenous forests (von Maltitz *et al.*, 2003), 26 forest types are currently recognised (Mucina & Geldenhuys, 2006). The Southern Afrotemperate Forest Group consists of three vegetation types: Southern Cape Afrotemperate Forest, Western Cape Talus Forest and Western Cape Afrotemperate Forest (Mucina & Geldenhuys, 2006). This study focuses on Western Cape Afrotemperate Forest, which occurs on the Cape Peninsula. Forest patches occur in deep ravines on all sides of Table Mountain, and in steep, sheltered cliffs on the plateau, but only extend onto open slopes on the moist, sheltered eastern side (Adamson, 1927).

Southern Afrotemperate Forest currently has the conservation status of ‘Least Threatened’ (Rouget *et al.*, 2004), because over half of the extant patches have statutory conservation in national parks (including Table Mountain National Park) and nature reserves (Mucina & Geldenhuys, 2006). However, this classification represents forest only at the level of forest groups, not types, thereby not accounting for differences in conservation status among forest types. Western Cape Afrotemperate Forest is one of the rarest forest types in South Africa, covering only 4731 ha (Berliner & Benn, 2003; Berliner, 2005). It has historically been heavily exploited, although in the absence of detailed scientific documentation it is impossible to know the precise extent of forest in the past, before human exploitation (McKenzie *et al.*, 1977). Consequently, Berliner (2005) recommended that the IUCN endangerment category for Western Cape Afrotemperate Forest should be ‘Vulnerable’. Berliner (2005) argued that, since no reliable scientific data are available to assess the levels of historic habitat loss for forest

types, habitat loss (transformation) should not be used as the main criterion for assessing the ecosystem status of forests in South Africa.

### *Fynbos or forest on the Cape Peninsula?*

Bioclimatically, most fynbos occurs in areas mesic enough to support Afrotropical forest. Bond *et al.* (2003), using a simulation study, argue that current levels of CO<sub>2</sub> (360 ppm) are potentially suitable for mesic fynbos to develop towards fire-sensitive forest, if fires were excluded. This is evident on the Cape Peninsula, in areas such as Kirstenbosch and Orange Kloof, where changes in fire management have allowed forest to colonise areas naturally covered with Granite Fynbos only a few decades ago (McKenzie *et al.*, 1977; Rebelo *et al.*, 2006). Succession to forest may be possible in areas of high rainfall, especially in old, moribund fynbos vegetation, where shading facilitates the establishment of forest species (Manders, 1990). However, under more natural conditions, fynbos maintains dominance in the landscape through regular natural burning, since fire excludes forest species (Rebelo *et al.*, 2006 and references therein). Consequently, 'true' evergreen Afrotropical forest is naturally confined to large screes, deep kloofs and fire refugia protected by cliffs and scarps. Fire is also responsible for the sharp (often only a few metres) ecotone between fynbos and forest (Rebelo *et al.*, 2006).

Nutrient availability also differs greatly between fynbos and forest. In fynbos, nutrient cycling is slow and fire acts as a mineralising agent, whereas in forest, nutrients are recycled in the litter layer (Stock & Allsopp, 1992; Rebelo *et al.*, 2006). The response of fynbos vegetation to low nutrient availability adds to its uniqueness and biological importance. This vegetation response includes serotiny, myrmecochory, obligate reseeding versus resprouting, lack of annuals, sclerophylly, lack of mycorrhiza and presence of cluster roots, carnivory and digestive mutualisms, low biomass of herbivores, and bird and mammal pollination (Rebelo *et al.*, 2006). Many of these are absent in the Afrotropical forest flora. Afrotropical forest differs physiognomically and floristically from fire-prone fynbos shrublands, because it contains medium to tall, closed-canopy, broad-leaved, evergreen trees and shrubs with strong Afro-tropical affinities, with most forest species widespread outside of the Cape Floristic Region (Cowling *et al.*, 1996). Southern Afrotropical Forest accounts for less than 5% of the plant species on the Cape Peninsula, with about half of the 150 plant species that are over 1.5 m tall occurring in fynbos (T. Rebelo pers. comm., 2008).

### *Pine plantation history on the Cape Peninsula*



Large-scale planting of pine and other fast-growing alien trees, such as eucalypt and acacia, in the Western Cape began in the 1850s. However, it was not until the 1880s that pine plantations were established on the slopes of Table Mountain and the Cape Peninsula (Cowling *et al.*, 1996; Richardson & Higgins, 1998). Commercial plantations were established in the fynbos surrounding forest patches, but rarely in areas cleared of evergreen forest (Mucina & Geldenhuys, 2006). Pine plantations on the eastern slopes are in Granite Fynbos, because Sandstone Fynbos productivity proved too low to sustain commercial plantations on the Cape Peninsula (T. Rebelo pers. comm., 2010).

Two species of pine (Family Pinaceae) have been widely planted for commercial timber production in the Western Cape. *Pinus pinaster* Ait. (Cluster pine) is native to Mediterranean areas of Europe (Henderson, 2001). It was introduced to South Africa in 1680 (Richardson *et al.*, 1992), soon after colonization of the Cape by the Dutch, and by 1772 was widespread on the Cape Peninsula (Richardson & Higgins, 1998). Cluster pine is now by far the most widespread invasive pine species in South Africa (Richardson *et al.*, 1994). It is also one of 15 woody plant species listed among the *100 of the world's worst invasive species* (Lowe *et al.*, 2000). *P. radiata* D. Don (Monterey pine or Radiata pine) is native to California in North America (Henderson, 2001). It was first recorded in the Western Cape in 1865 (Richardson & Higgins, 1998), where it quickly became the most commonly planted timber species (Lavery & Mead, 1998). Today, Monterey pine is the dominant exotic softwood used in plantations for commercial timber production in South Africa (Simberloff *et al.*, 2010), Australia (Sinclair & New, 2004) and New Zealand (Pawson *et al.*, 2008). Consequently, Monterey pine is the most widely planted alien conifer in the world, occupying over three million hectares of plantations outside of its natural range (Richardson *et al.*, 1994).

Both *P. pinaster* and *P. radiata* are successful alien invasives in Australia, New Zealand, Chile and South Africa (Richardson *et al.*, 1994), especially in fynbos (Richardson & Higgins, 1998). Both species are also declared invaders (category 2: commercially used plants) in South Africa (Henderson, 2001). Pines and other alien plants have been recognised as invasive species in fynbos since the 1920s (Rebelo *et al.*, 2006). *P. radiata* is also known to invade forest gaps (Henderson, 2001), but severe disturbance is needed to assist seedling recruitment in native forest, since by virtue of their structure, forests resist invasion (Richardson *et al.*, 1994). Consequently, Afrotropical forest is less vulnerable to invasion by pine than fynbos, even when forest patches are adjacent to pine stands (Richardson *et al.*, 1994).

Although facilitated by their long planting history, the life history strategies of these two pine species have largely determined their invasion success. Their good dispersal ability (small

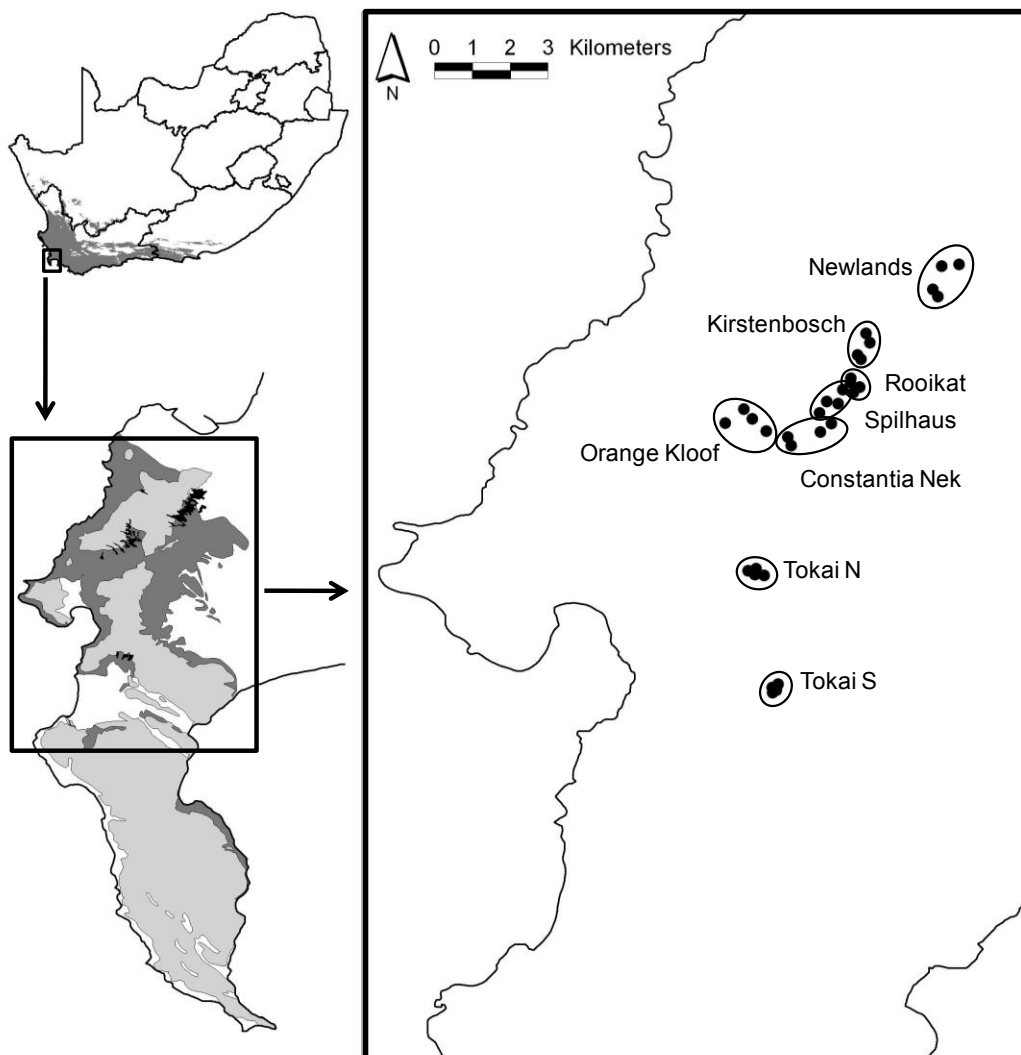
seeds, low seed-wing loading and long distance wind dispersal) facilitates invasion (Richardson *et al.*, 1990). In addition, their superior fire-resilience, compared with indigenous species, enables pines to persist and disrupt the natural non-equilibrium system (Richardson *et al.*, 1990). Fire-resilience is achieved by a combination of rapid growth to maturity and accumulation of large seed reserves in the canopy (Richardson & Cowling, 1992). Pines have a tendency to form dense thickets, and often out-compete fynbos shrubs in areas recovering from fire (Richardson *et al.*, 1994). Most pine seedlings establish in the first two years after fire in fynbos, when native plant cover is low (Richardson & Cowling, 1992).

Increasing alien plant invasions pose the greatest threat to biodiversity on the Cape Peninsula (Richardson *et al.*, 1996). The invasive spread of alien woody species from commercial plantations into adjacent native vegetation threatens areas set aside for conservation (Armstrong *et al.*, 1998), such as Table Mountain National Park. This has important management implications, where biodiversity conservation is a primary objective. Local extinction of many fynbos plant species has been reported following pine invasion (Richardson & van Wilgen, 1986; Richardson *et al.*, 1989). Most fynbos species are unable to withstand shading under pine, although some native geophytes, including *Ornithogalum* and *Moraea*, do persist (Adamson, 1927). This has implications for native plant and animal distributions, and for the rehabilitation of clear-felled pine areas. Pine plantations at Cecilia and Tokai plantations on the Cape Peninsula are currently being clear-fell harvested over a 20-year period, ending in 2025, with the intention of restoring the land to fynbos.

## **Study sites**

Thirty-two sites were selected at eight localities across the eastern slopes of Table Mountain National Park, which lies within the northern section of the Cape Peninsula (Fig. 2.1, Appendix A). These sites were located, from north to south, in Newlands Forest, Kirstenbosch National Botanical Garden, Cecilia Plantation, Orange Kloof Forest Station and Tokai Plantation, with roughly 12 km between the northern- and southern-most sites. The eight clusters, each consisting of four sites, were selected to replicate each of the four 'vegetation types' or habitats: (1) Western Cape Afrotropical Forest, (2) Peninsula Sandstone Fynbos or Peninsula Granite Fynbos, (3) commercial pine plantation (*Pinus pinaster* or *P. radiata*) and (4) recently clear-felled pine plantation. The 'ideal' scenario of forest, fynbos, pine plantation and clear-felled pine sites together in one area was only possible at Rooikat and Spilhaus Ravines in Cecilia Plantation, and Tokai N (Boekenhoutkloof) and Tokai S (Prinskasteel) in Tokai Plantation. The

remaining four areas had two sites of the same habitat to make up a total of eight replicates per habitat. Where two sites of the same habitat were sampled in an area, these sites were not contiguous, to avoid pseudoreplication. Sites were *a priori* selected based on vegetation and not on the presence-absence of alien invertebrate species.



**Figure 2.1.** Location of 32 study sites in Table Mountain National Park (right) on the Cape Peninsula, South Africa. Map of South Africa (top left) shows the Fynbos Biome (in grey). Cape Peninsula (bottom left) shows the distribution of native vegetation sampled: Peninsula Sandstone Fynbos (light grey), Peninsula Granite Fynbos (dark grey) and Western Cape Afrotemperate Forest (black). See Appendix A for site information.

## Pilot study

A pilot study was conducted at Cecilia in mid May 2008 (late autumn, after the first winter rains). The aim was to determine the minimum number of replicates for each collecting method (*i.e.* sampling intensity) needed to adequately represent the ground-dwelling invertebrate community, within reason of practical limitations. One site each in contiguous Afrotropical forest (Site 9, Rooikat Ravine), Sandstone Fynbos (Site 10) and pine plantation (Site 11) was sampled for ground-dwelling invertebrates (see Appendix A for site details). At each site, five leaf litter samples, 10 soil samples, 10 pitfall traps, 10 sugar-baited ant traps and one decayed log sample were collected (see full-scale study sampling methods below for details).

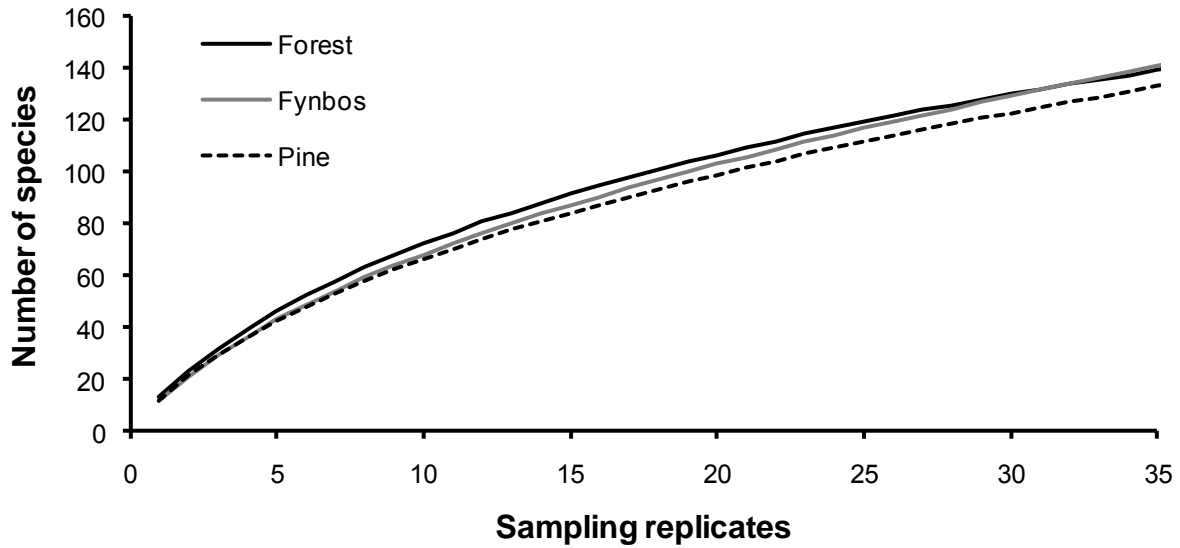
To justify the use of both unbaited (antifreeze) and sugar-baited pitfall traps, the total number of ants collected in each habitat was compared (Table 2.1). Number of individuals was consistently higher in sugar-baited traps across habitats, suggesting that ants may be attracted by the sweet scent of a carbohydrate source (sugar solution), even if most individuals cannot return to the colony to recruit more nestmates to the sugar solution. Greenslade & Greenslade (1971) also report much higher catches of ants in syrup (sugar in water) baited traps (800 individuals) compared to control (alcohol-glycerol) traps (four individuals).

**Table 2.1.** Total number of ant individuals collected in 10 pitfall traps versus 10 sugar-baited ant traps in each habitat during the pilot study, with the number of species collected in parentheses.

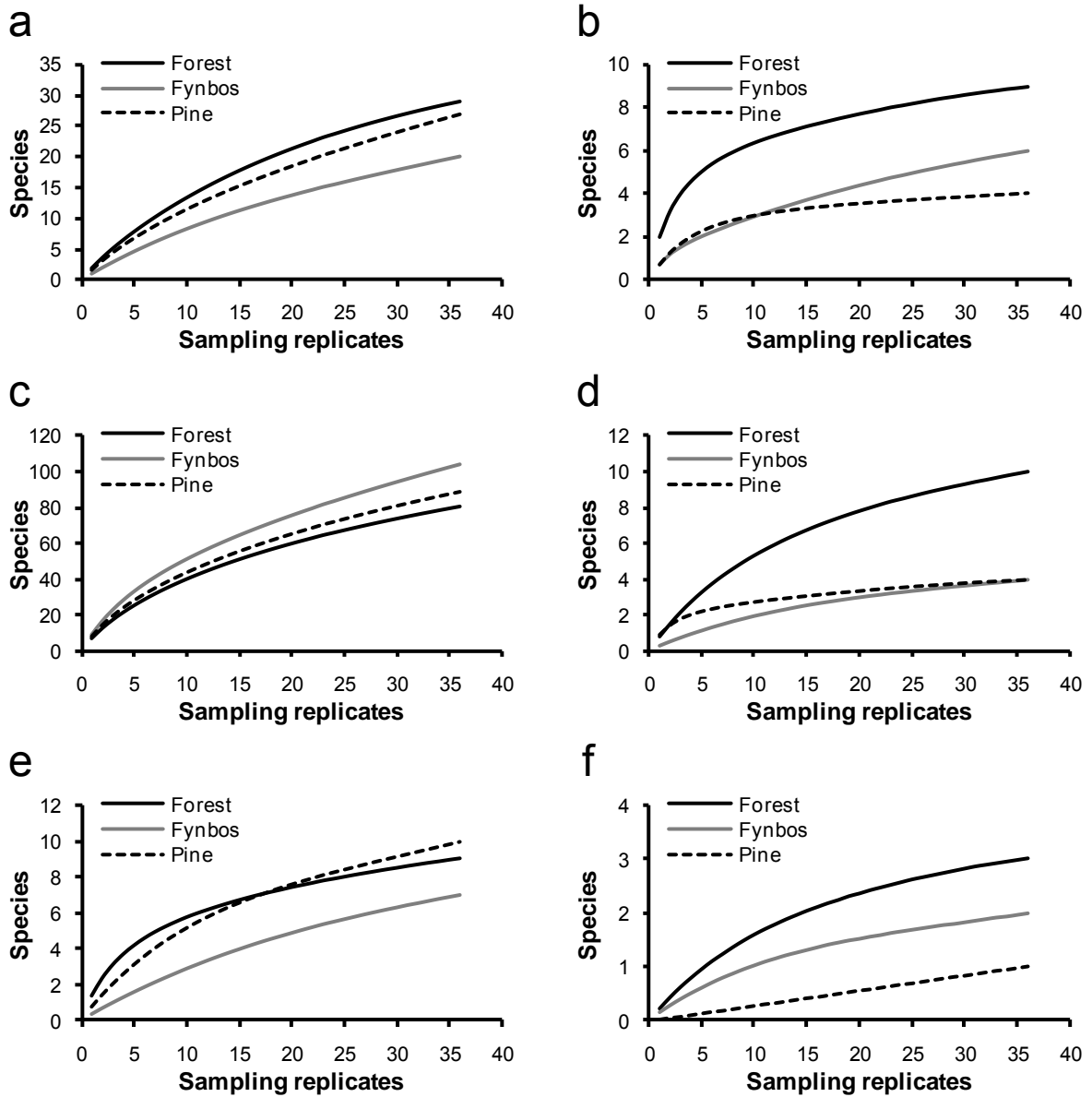
Habitat	All ants		Argentine ants only	
	Pitfalls	Baited ant traps	Pitfalls	Baited ant traps
Forest	32 (8)	1241 (8)	0	7
Fynbos	149 (10)	1938 (15)	15	1399
Pine	93 (5)	2078 (8)	18	1764

Sample-based randomized species-accumulation curves (Gotelli & Colwell, 2001) were plotted using  $S_{obs}$  Mao Tau, calculated in EstimateS version 8 (Colwell, 2006), to test sampling saturation. Sampling intensity was fairly low and as a result sampling saturation was not fully achieved for all species combined (Fig. 2.2), higher invertebrate taxa (Fig. 2.3), or sampling methods (Fig. 2.4). However, it should be appreciated that sampling saturation is seldom achieved for multi-taxa terrestrial invertebrate surveys, even following intensive sampling

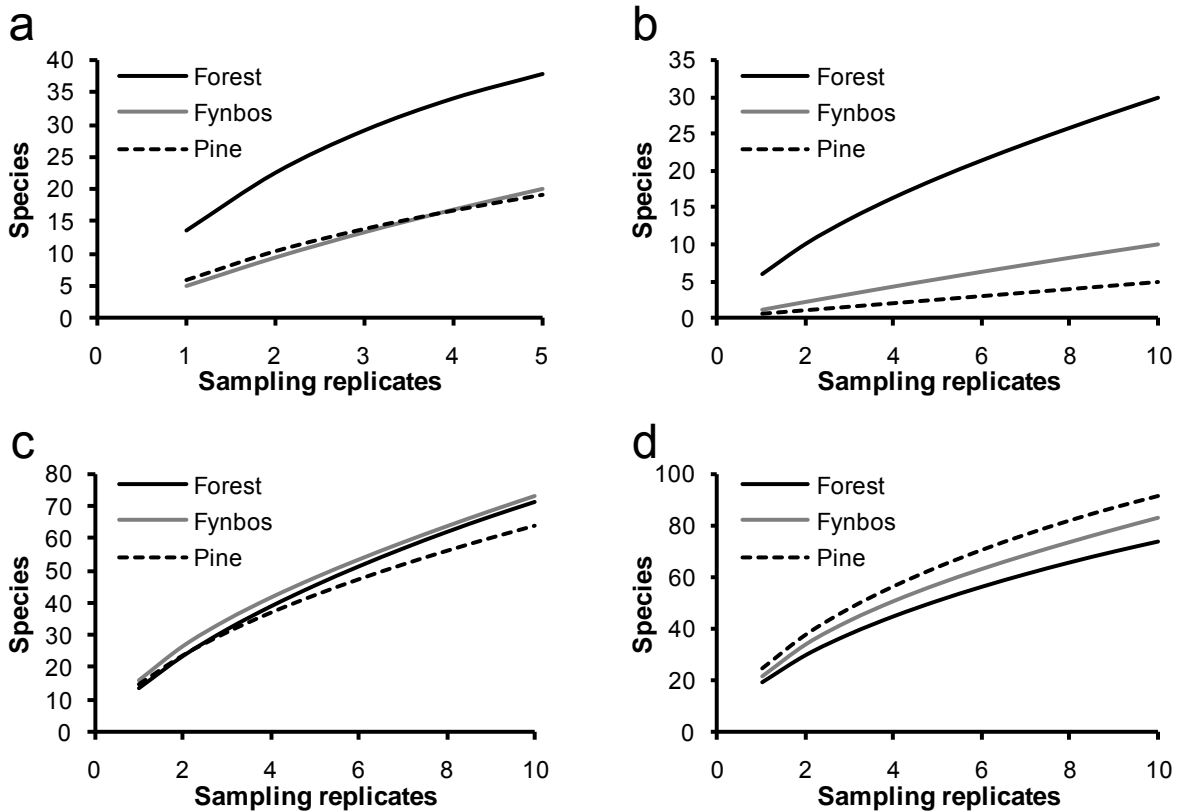
(Gotelli & Colwell, 2001), and sampling intensity is therefore a trade-off against logistical, time and cost constraints. Most of the Afrotropical forest patches on the Cape Peninsula are small and dominated by edge effects, so that the core habitat area available and accessible for sampling prohibited increasing the number of replicate samples collected.



**Figure 2.2.** Species-accumulation curves of all species and pilot study collecting methods combined. Curves were calculated in EstimateS using  $S_{obs}$  (Mao Tau) and the classic formula for Chao 1 and Chao 2, randomized 50 times.



**Figure 2.3.** Species-accumulation curves for pilot study invertebrate higher taxa: (a) Arachnida, (b) Crustacea, (c) Insecta, (d) Mollusca, (e) Myriapoda and (f) Oligochaeta.



**Figure 2.4.** Species-accumulation curves for all pilot study invertebrate species for (a) leaf litter samples, (b) soil samples, (c) pitfall traps and (d) sugar-baited ant traps. Log samples omitted, because only one log per site was sampled.

The pilot study assisted in (a) gaining insight on the number and groups of invertebrates to be collected and (b) refining the proposed collecting methods and sampling intensity (number of replicates per site). Besides doubling the number of leaf litter (from five to ten) and decayed log (from one to two) replicates per site, the same protocols from the pilot study were used in the full-scale study. This decision was based on the practical constraints of carrying additional equipment (especially traps and liquid) up the mountain, and the extra time required both in the field and for subsequently processing and identifying samples in the laboratory.

Although the pilot study took place at a different time of year to the full-scale sampling, this was not expected to have a pronounced impact on the reliability of interpretation of findings. Seasonal effects on invertebrate communities in southern Africa are less pronounced than in more temperate regions of the world, especially when compared to the Northern Hemisphere. Furthermore, ground-dwelling invertebrates (earthworms, centipedes, millipedes, molluscs and

ants) in Afrotropical forest in the Drakensberg mountains show seasonal stability, with the invertebrate community sampled in winter a subset of the summer community (Uys *et al.*, 2010).

## Sampling methods

### *Full-scale study sampling methods*

Sites were selected in the approximate centre of a patch of vegetation, depending on accessibility. At each of the 32 sites (except Site 11), a range of sampling methods, both active and passive, was employed to sample ground-dwelling invertebrates. These methods included leaf litter samples, soil samples, pitfall traps, sugar-baited ant traps and decayed logs. The focus of this study is on epigeic invertebrates, because of their high levels of endemism on the Cape Peninsula, their vulnerability to disturbance and habitat loss, and their appropriateness to answering questions posed by this thesis. While the sampling methods chosen primarily targeted epigeic invertebrates, hypogaeic taxa were collected in soil samples. Sampling did not target flying insects, but incidental catches of foliage-dwelling and aerial taxa that did occur were not excluded from analyses.

Twenty-five days were spent in the field, sampling between 08h00 and 14h00 (*i.e.* 150 sampling hours). The order in which the eight clusters of sites were sampled was randomly chosen and different in 2008 and 2009, to avoid possible unwanted spatial autocorrelation (Legendre, 1993) between the north-south alignment of sites and the date of sampling. Leaf litter and soil sampling took place from mid September to late November 2008 (*i.e.* spring to early summer). Pitfall trap, sugar-baited ant trap and decayed log sampling took place from early January to late February 2009 (*i.e.* late summer, dry season). Sampling took place at different times of year for two reasons. Firstly, for the practical limitations of processing samples and secondly, to maximise the community sampled, since many litter taxa are most abundant at the end of the rainy season, yet ants are most active and abundant during summer. The entire block of pine plantation at Site 11 (Rooikat, Cecilia) was unexpectedly felled in January 2009, ahead of the forestry company's proposed felling schedule, so no pitfall traps, ant traps, or decayed logs were sampled there, and this site was omitted from subsequent analyses.

Ten leaf litter samples per site were collected to sample leaf litter invertebrates, by filling a 2 l container with leaf litter every 5 m along a transect. Ten soil samples per site were collected to sample soil invertebrates. One 500 ml soil sample was taken every 5 m along a transect, by clearing away surface vegetation and litter, digging a hole with a small trowel, and removing soil up to 150 mm depth. Litter and soil samples were stored in sealed plastic bags



and kept cool (in a constant environment room set at 10°C) to minimize decomposition and invertebrate mortality, and to immobilize predaceous animals, until samples were sorted. All samples were sorted within two weeks, and mostly within a few days, of collection. Samples were sorted in a random order to avoid any habitat-bias in time spent in cool-storage, which could lead to variance in the results obtained. Given the potential limitations of this cool-storage delay prior to sampling, litter and soil samples were sorted meticulously by hand. Hand-sorting was chosen instead of using winkler bags, Burlese funnels or some other extraction method that relies on the assumption that all invertebrates present in the sample are alive and able to move away from a light/heat source, and in doing so fall into a collecting jar. During hand-sorting, all vegetation (for leaf litter samples) or soil (for soil samples), and the inside of each bag, were thoroughly and meticulously inspected with the aid of a desk lamp for illumination and to warm up the animals. All invertebrates larger than 0.5 mm were removed and preserved. Mortality was very low, even for small, soft-bodied taxa, such as springtails.

Ten pitfall and 10 ant traps per site were left in the field for seven days to collect ground-dwelling invertebrates not easily sampled using other methods. Pitfall traps were 450 ml round, clear plastic tubs (85 mm deep and 100 mm diameter opening), half filled with 50% ethylene glycol (antifreeze) and placed at 5 m intervals along a transect. Every second tub was covered with an inverted plastic flower pot drip tray (160 mm diameter), raised 100 mm above ground level on a wire frame, to reduce evaporation, prevent rain from flooding the traps and limit the quantity of leaves and twigs that fell into the tub. Only half the traps were covered due to the logistic constraints of carrying equipment up the mountain. Sugar-baited ant traps were set to specifically target ants that are attracted to a carbohydrate source. Ant traps used the same plastic tubs and covers as pitfall traps, and were left in the field for the same seven days. Ant trap tubs were placed at 5 m intervals along a transect that ran parallel to, but 5 m from, the pitfall traps. Tub were half filled with a 20% sucrose solution. All invertebrates collected in the pitfall and ant traps were thoroughly rinsed in tap water before preservation.

Two decayed logs of approximately 1.5 m length and 0.2 m diameter, in an advanced state of decay, were selected at each site to sample saproxylic invertebrates. Each log was transferred to a large, white, plastic sheet, and sorted in the field by systematically breaking apart the entire log, removing and preserving all invertebrates (1 mm and larger) visible to the naked eye. Sampling was restricted to mornings, because the eastern slopes of the mountain are in shadow by mid-afternoon. Logs were carefully moved on the plastic sheet to a clearing or path nearby for maximum light and ease of sampling. Only two logs per site were sampled, both

because of time constraints (logs had to be sorted on site) and because of the low number of suitably decayed logs (especially in fynbos) available.

*Environmental variables*

Basic environmental variables were recorded at all 32 sites. GPS coordinates were recorded in the field using a hand-held Garmin GPS and checked against Google Earth 5.0. Altitude (elevation) recorded in the field proved unreliable, so mean altitude was taken from the 1:20 000 Table Mountain hiking map (Slingsby, 2007). The habitat at each site (1000 m<sup>2</sup>) was visually scored according to canopy cover (%), ground cover (%), leaf litter (%), rocks (%) and shrubs less than 1 m (%) and summarised for each vegetation type (Table 2.2).

**Table 2.2.** Descriptive statistics for visually scored percentage cover in each habitat.

Habitat	Canopy cover (%)	Groundcover (%)	Leaf litter (%)	Rocks (%)	Shrubs (%)
<b>Mean ± SD</b>					
Forest	80.00 ± 13.09	46.25 ± 26.69	83.75 ± 11.88	50.63 ± 27.57	37.50 ± 19.09
Fynbos	23.75 ± 24.46	62.50 ± 44.32	62.50 ± 23.75	17.50 ± 16.69	63.75 ± 31.59
Pine	70.00 ± 17.32	27.14 ± 22.89	95.71 ± 7.87	22.14 ± 15.77	22.86 ± 17.99
Felled	0	50.63 ± 41.27	43.75 ± 33.78	16.88 ± 10.67	4.38 ± 4.96
<b>Range</b>					
Forest	60 - 100	10 - 80	70 - 100	5 - 80	0 - 60
Fynbos	0 - 70	0 - 100	20 - 90	0 - 40	40 - 100
Pine	50 - 90	0 - 50	80 - 100	0 - 50	0 - 50
Felled	0	5 - 100	10 - 100	5 - 30	0 - 10

Soil pH, moisture and organic content were measured in the laboratory. Soil samples were weighed in their sealed bags within 24 hours of collection, using a 600 g balance, to determine “wet weight”. Soil pH was measured by mixing 12.5 ml of soil in 12.5 ml distilled water, shaking the mixture for 30 seconds, allowing it to settle for five minutes, and measuring the pH of the supernatant liquid with a hand-held Crison pH meter. Mean soil pH was calculated for five randomly chosen soil samples per site.

After removing all invertebrates from each sample, all soil was returned to the plastic bag and re-weighed to account for any loss (typically up to 10 g loss, largely due to removal for pH measurement). This new weight was used as the wet soil weight. Open plastic soil bags

were dried in an oven at 60°C for at least 36 h. Dry soil was weighed to determine weight loss due to moisture content of the soil. Soil moisture was calculated as:

$$\text{Soil moisture} = (\text{wet weight} - \text{dry weight}) / (\text{wet weight})$$

Soil samples were large (greater than the standard 40 g samples) and not dried at over 105°C. This is acknowledged as a limitation of this study and may have affected soil moisture comparisons, especially for sites with high clay content in the soil, which would have lost their pore water, but not their adsorbed water.

Soil organic content was measured by further drying soil samples in a muffle furnace at 400°C for 4 h, to burn off all organic content (including roots, twigs and leaves) in the soil. Soil was then cooled to room temperature and weighed. Soil organic content was calculated as:

$$\text{Soil organic content} = (\text{dry weight} - \text{muffle dried weight}) / (\text{dry weight})$$

Despite the high range of values (Table 2.3), one-way analysis of variance (ANOVA) showed significant differences between habitats for soil pH ( $F = 36.654$ ,  $df = 3$ ,  $p < 0.001$ ) and soil moisture ( $F = 19.062$ ,  $df = 3$ ,  $p < 0.001$ ). Due to technical failure of the muffle furnace, soil organic content was only calculated for Sites 1 to 11. No significant difference ( $F = 0.471$ ,  $df = 2$ ,  $p = 0.641$ ) in soil organic content was found between forest ( $n = 4$  sites), fynbos ( $n = 4$  sites) and pine plantation ( $n = 3$  sites), probably due to high variance within sites. Soil organic content was therefore considered an unreliable explanatory variable and not used in analyses.

**Table 2.3.** Descriptive statistics for soil pH, moisture and organic content in each habitat.

Habitat	pH				Moisture (%)				Organic content (%)			
	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD
Forest	4.6	6.9	6.15	0.53	9.2	70.9	32.19	13.80	2.6	74.8	24.57	18.50
Fynbos	4.2	6.7	5.56	0.55	2.3	56.5	18.04	11.90	4.8	85.3	18.31	19.19
Pine	4.5	6.5	5.50	0.48	5.2	71.4	33.33	14.95	9.1	81.5	28.12	16.06
Felled	4.3	5.9	4.99	0.42	2.1	70.4	25.71	16.70				

#### *Invertebrate identification*

All invertebrates, except earthworms and moths (for the full-scale study) and unidentifiable nymphs and larvae (for both the pilot and full-scale studies), were sorted to morphospecies using easily recognisable morphological differences (*sensu* Oliver & Beattie, 1996). As many taxa as possible were sent to specialists for further identification (Appendix B). Roughly 20% of all morphospecies were not checked or identified further by an expert as none was available. Consequently, some unknown degree of identification error is inevitable in these data, with

accuracy dependent on prior experience with different taxa and the availability of identification keys. Nevertheless, any error in identifications should be consistent across habitats. Morphospecies are referred to as species hereafter. The reference collections for taxa identified by experts have been deposited in the respective museums of their home countries, while a reference collection of the remaining taxa has been deposited in the Iziko South African Museum, Cape Town.

## CHAPTER 3. THE INFLUENCE OF ALIEN PINE PLANTATIONS ON INVERTEBRATE DIVERSITY AND SPECIES TURNOVER ON THE CAPE PENINSULA

### Introduction

Plantations are popularly considered 'biological deserts' (Bonham *et al.*, 2002; Hartley, 2002; Brockerhoff *et al.*, 2008) and perceived to support impoverished faunal diversity, compared to nearby native forests (Lachat *et al.*, 2006). A global review of biodiversity in plantations revealed a general trend (94% of studies) of lower diversity of invertebrates, birds, mammals and plants in single-species exotic plantations, compared to natural forests (Stephens & Wagner, 2007). Furthermore, 57% of studies comparing exotic plantations to non-forested natural ecosystems, such as grasslands and fynbos, also report lower diversity in plantations (Stephens & Wagner, 2007). In the Brazilian Amazon, lower species richness in exotic plantations compared to primary rainforest has been reported for birds (Barlow *et al.*, 2007a), lizards and amphibians (Gardner *et al.*, 2007), and dung beetles (Gardner *et al.*, 2008). Lower species richness in exotic conifer plantations, compared to native *Nothofagus* forest, has also been reported for native birds in New Zealand (Clout & Gaze, 1984) and for understory plants, epigeal beetles and birds in Argentinean Patagonia (Paritsis & Aizen, 2008).

Similar trends are apparent for South African plantations. Ant diversity (Donnelly & Giliomee, 1985) and bird diversity (Armstrong & van Hensbergen, 1994) are lower in pine plantations than in fynbos, the Mediterranean-type shrubland in the Western Cape Province. On the Cape Peninsula, pine plantations support low native plant diversity (Cowling *et al.*, 1979) and low invertebrate diversity (Pryke & Samways, 2009b). Species richness of litter invertebrate communities in pine plantations may be half that of contiguous Afrotemperate forest (Ratsirarson *et al.*, 2002; Raharinjanahary, 2007). In KwaZulu-Natal Province, similar trends of reduced diversity in plantations have been reported for grasshoppers (Samways & Moore, 1991), butterflies (Wood & Samways, 1991), ground-dwelling invertebrates (Samways *et al.*, 1996), spiders (van der Merwe *et al.*, 1996) and birds (Armstrong & van Hensbergen, 1995; 1996). Likewise, in Mpumalanga Province, plantations have a negative impact on grassland bird diversity, especially globally threatened species (Allan *et al.*, 1997). However, it should be noted that diversity in plantations is not always as low as expected. Samways *et al.* (1996) report lower (but not significantly so) species richness under several invasive alien plant species, compared to native vegetation.

In addition to impoverished species richness, the composition of invertebrate community assemblages in exotic plantations often differ from those of adjacent native vegetation (e.g. Samways *et al.*, 1996; Barlow *et al.*, 2007b). Plantation communities are often dominated by widespread, generalist species (Magura *et al.*, 2000; Sinclair & New, 2004; Gardner *et al.*, 2007; Brockerhoff *et al.*, 2008). Furthermore, several native species may be absent in exotic plantations (Tattersfield *et al.*, 2001; Bonham *et al.*, 2002). This is relevant for conservation, especially when the species absent in plantations include rare, endemic taxa.

The impact of alien plantations is expected to be particularly severe in areas supporting exceptional invertebrate diversity and endemism, such as the Cape Peninsula (Picker & Samways, 1996). The Cape Peninsula's distinctive invertebrate assemblage is of global significance (Cowling *et al.*, 1996) and zoogeographic importance (Jarvis, 1979). Picker & Samways (1996) identified 111 endemic invertebrate species on the Cape Peninsula, with strong patterns of endemism evident in certain invertebrate groups, such as harvestmen, velvet worms and cave Crustacea. The Cape Peninsula boasts the second highest (after Pietermaritzburg) millipede species richness and site endemism in South Africa (Hamer & Slotow, 2002), although this may be an artefact of collection bias, as previous researchers have been based at these locations. Cape Peninsula endemics are mostly palaeo-endemic, Gondwanan relictual taxa, with few surviving relatives (Picker & Samways, 1996). Most Table Mountain endemics are associated with palaeogenic zones: sandstone caves, forested slopes and streams (Picker & Samways, 1996). Sandstone caves on the Cape Peninsula alone support 21 endemic invertebrate species, far more than any other cave system in southern Africa (Sharratt *et al.*, 2000).

The most inclusive available list of invasive alien animals in South Africa lists 601 species of vertebrates and invertebrates (Picker & Griffiths, 2011). This is most certainly an underestimate, although the number is unlikely to exceed 2500 introduced species, based on inventories from other regions: 1590 terrestrial alien invertebrates recorded in Europe (Roques *et al.*, 2009), over 2000 alien arthropod species from the continental USA, over 2500 species recorded in Hawaii (Pimentel, 2002) and 2200 from New Zealand (Barlow & Goldson, 2002). The state of taxonomic knowledge of alien, and indeed native, invertebrates varies greatly among invertebrate taxa. Molluscs, like arthropods, are comparatively well-studied. In South Africa, there are 34 introduced species of terrestrial mollusc, of which 28 have established and 20 have been collected in the greater Cape Town area (Herbert, 2010). Raharinjanahary (2007) recorded 16 species of alien saproxylic (wood-inhabiting) invertebrates in Newlands Forest on the Cape Peninsula, including earthworms, snails, slugs, woodlice, earwigs and ants. The South

African National Parks (D. Spear pers. comm., 2010) and South African National Biodiversity Institute (T. Rebelo pers. comm., 2011) species databases collectively have records for 60 alien invertebrate species on the Cape Peninsula. However, not all of these alien species have been recorded inside the national park, several are dubious records, and many are flying insects. Consequently, there is an urgent need for a systematic, quantified survey of ground-dwelling alien invertebrates in Table Mountain National Park. These alien invertebrates may further impact the native invertebrate diversity, either directly, through predation and parasitism, or indirectly, by disease transmission, disrupting mutualisms and through interference competition (Kenis *et al.*, 2009).

Facilitative and mutualistic interactions among introduced species can lead to ecological impacts on native species that are more pronounced and accelerated than would be expected if the invasive species did not act in concert; and there are many examples illustrating this in the invasion literature (Simberloff, 2006). Plantations, like woody invasive stands, modify habitat and may also facilitate the establishment and spread of invasive alien invertebrates (Lawrence, 1953). These alien invertebrate species could subsequently penetrate pristine ecosystems through corridors of invasive plants. In South Africa the forestry industry is recognized as a chief agent in the dispersal of terrestrial alien mollusc species into remote areas, where they have subsequently spread into pristine habitats (Herbert, 2010). Invasive ants throughout the world also readily spread from human-modified habitats into undisturbed natural areas, when abiotic conditions are suitable (reviewed in Krushelnycky *et al.*, 2010). The Argentine ant, *Linepithema humile*, occupies roughly half of South Africa's land surface area and is well established in protected areas (Luruli, 2007), including in Table Mountain National Park on the Cape Peninsula (Skaife, 1961; Ratsirarson *et al.*, 2002; Raharinjanahary, 2007; Pryke & Samways, 2010). Argentine ant sub-colonies are known to spread into Afrotropical forest (Ratsirarson *et al.*, 2002) and mountain fynbos (Christian, 2001), but it remains unclear whether they can establish more permanent colonies in undisturbed fynbos (Macdonald & Jarman, 1984; De Kock & Giliomee, 1989), as the majority of native habitats invaded are in close proximity to plantations, or other sites subject to anthropogenic change.

This study was undertaken on the Cape Peninsula in Table Mountain National Park (Cape Town), a World Heritage Site and global biodiversity hotspot in the Cape Floristic Region. On the Cape Peninsula, exotic pine plantations were established in the 1880's for commercial timber production (Cowling *et al.*, 1996; Richardson & Higgins, 1998). These pine plantations were largely established in Granite Fynbos (Mucina & Geldenhuys, 2006), but many Afrotropical forest litter invertebrate species have colonised these plantations.

The aim of this study is to assess the impact of exotic pine plantations on ground-dwelling invertebrate diversity (species richness and abundance) and species turnover. Firstly, pine plantations are hypothesized to support lower invertebrate species richness and abundance, compared to surrounding (often contiguous) Afrotropical forest and fynbos. Based on the findings of Ratsirarson *et al.* (2002) and Raharinjanahary (2007), species richness in pine plantations is predicted to be at least half that of Afrotropical forest. Pine plantations are further predicted to (a) be more similar in species richness to fynbos than to forest, based on the findings of Stephens & Wagner (2007) and (b) to support a lower number of Cape Peninsula endemics than forest, but have a greater representation of alien species. Secondly, the invertebrate community in pine plantations is hypothesized to be more similar to that of forest than to that of fynbos; even though these pine plantations originally replaced Peninsula Granite Fynbos (T. Rebelo pers. comm., 2010). Plantations provide litter and dead wood microhabitats that broadly mimic those in forest, often supporting native forest invertebrate species. These pine plantations are predicted to support a mixed invertebrate community derived from both native habitats, but showing a closer similarity to the forest community than the original habitat, fynbos. As a consequence of their reduced plant diversity, plantations may offer fewer niches or microhabitats, and consequently display lower beta diversity than more species rich and heterogeneous native vegetation types. Thus pine plantations are predicted to have lower beta diversity or species turnover between sites than both Afrotropical forest and fynbos, in terms of their invertebrate communities.

## Methods

### *Study sites and collecting methods*

Refer to Chapter 2 and Appendix A for the location of the sites sampled and collecting methods used in Western Cape Afrotropical Forest (n = 8 sites), fynbos (n = 8 sites: six Peninsula Sandstone Fynbos and two Peninsula Granite Fynbos) and pine plantation (n = 7 sites) in Table Mountain National Park. Site 11 (pine plantation in Cecilia) was omitted from all analyses, because it was unexpectedly clear-felled in January 2009, ahead of the Mountain to Ocean (MTO) Forestry Pty (Ltd) proposed felling schedule. Consequently, no pitfall traps, sugar-baited ant traps, or decayed logs were sampled at Site 11, compromising its comparability with other sites. For each of the other 23 sites, data from the replicates (10 leaf litter, 10 soil, 10 pitfall trap, 10 sugar-baited ant trap and two decayed log samples) were pooled for a single species richness value per site, to avoid problems of pseudoreplication (Hurlbert & Hurlbert, 2004),



inherent spatial autocorrelation within sites (Legendre & Legendre, 1998) and differences in catches amongst collecting methods. Refer to Appendix C for a list of species collected in each habitat.

#### *Species richness and abundance analyses*

Raw species richness (number of species) and abundance (number of individuals) in each habitat were tallied for all invertebrate taxa combined, individual insect orders and non-insect classes. Relative species richness and relative abundance in each habitat were each expressed as a percentage of the total number of individuals collected for insect orders and non-insect classes.

Species-accumulation curves for the observed species richness of forest, fynbos and pine plantation were calculated using  $S_{obs}$  Mao Tau sample-based rarefaction curves, randomised 50 times in EstimateS version 8 (Colwell, 2006). The x-axis of these sample-based rarefaction curves was re-scaled from sites sampled to individuals. Observed species richness counts were re-scaled to obtain abundance-standardised species richness, using the lowest number of individuals collected in a habitat (19 614 individuals in pine plantation). Re-scaling is necessary when curves do not reach an asymptote and/or there is overlap in the 95% confidence intervals, because individual densities vary among samples and species rich invertebrate communities are impractical to sample exhaustively (Gotelli & Colwell, 2001; Colwell *et al.*, 2004). Estimated total species richness based on abundance (ACE) and incidence (ICE) was also calculated for forest, fynbos and pine plantation in EstimateS. Both sample-based and abundance-standardised estimated species richness were calculated. The non-parametric coverage-based species richness estimators, ACE (abundance-based coverage estimator) and ICE (incidence-based coverage estimator) recognise the contribution of rare (less than 10 individuals) species (Magurran, 2004).

Observed species richness counts were re-scaled to obtain abundance-standardised species richness, using the lowest number of individuals collected at a site (1340 individuals), in EstimateS. Site 25 (forest) and Site 26 (fynbos) were omitted from analyses of re-scaled species richness, because they each had a minimum number of individuals greater than the 1340 individuals cut-off chosen for abundance-standardisation. Mean species richness per site was calculated for each habitat, for both observed species richness and abundance-standardised species richness, using STATISTICA version 9 (StatSoft, Inc., 2009). One-way analysis of variance (ANOVA) was performed to test for differences in the observed species richness and abundance-standardised species richness amongst forest, fynbos and pine

plantation in STATISTICA. Mean abundance per site was calculated for each habitat, and compared between sites using a Kruskal-Wallis (ANOVA by ranks) test in STATISTICA, since the abundance data were not normally distributed.

Species-rank abundance curves, also known as dominance plots, were plotted for each habitat in PRIMER version 6 (Clarke & Gorley, 2006), to determine if there was greater dominance in one habitat. For each habitat, data were pooled across sites, species were then ranked in order of importance along the x-axis on a log scale, and their percentage contribution to the total was plotted along the y-axis. The x-axis was log transformed for better visualisation of the more common species. Typically, most ecological communities have only a few very abundant species and many rare species (Magurran, 2004). Dominance, or species evenness, can be visually inferred from the slope of the rank-abundance curve (McGill *et al.*, 2007). Steep gradients indicate low species evenness, because the high-ranking species have much higher abundance than low-ranking species (Magurran, 2004).

#### *Community composition and species turnover analyses*

A triangular matrix of Bray-Curtis dissimilarity of  $\log_e(x + 1)$  transformed community composition between sites was used to map the interrelationships of invertebrate communities in cluster analysis using complete linkage clustering, and in ordination by non-metric multidimensional scaling (MDS), in PRIMER. Data were log-transformed to down-weight highly abundant species. Matrices were also constructed for alternative transformations (square root, fourth-root and presence-absence), but all gave similar results to log-transformed distance, and hence results from those analyses are not reported. Cluster analysis is a simple and intuitively meaningful method used to find natural grouping of samples or sites (Magurran, 2004). MDS is also widely used for graphical representation of community relationships because of its conceptual simplicity, flexibility, dependence only on a biologically meaningful view of the data, independence of normally distributed data with equal variance between samples, and its distance preserving properties (Clarke, 1993; Clarke & Warwick, 2001). In an MDS plot, the x-axis represents the direction of maximum variation, with the position of samples (or sites in this case) reflecting their dissimilarity. Clusters in an MDS plot are delimited according to the percentage dissimilarity among sites in cluster analysis. The stress value acts as a measure of reliability, since the risk of drawing false inferences from an ordination increases with greater stress. Stress values of less than 0.2 are considered reliable.

The same Bray-Curtis dissimilarity matrix of log-transformed data was used for pairwise analysis of similarity (ANOSIM), to test the null hypothesis of no difference in invertebrate

community composition amongst forest, fynbos and pine plantation. ANOSIM is the non-parametric, multivariate equivalent of ANOVA, applied to the rank dissimilarity matrix using a permutation procedure (999 permutations), in PRIMER (Clarke & Green, 1988). It calculates the  $R$  statistic, which provides a relative measure of separation of predefined groups. The  $R$  statistic ranges from +1 (all samples within groups are more similar to one another than to any samples from another group) to -1 (all samples within groups are more similar to samples from another group than to other samples within the group). An  $R$  statistic of zero indicates no difference among groups (*i.e.* the null hypothesis of completely random grouping).  $R$ -values  $> 0.75$  are considered well separated groups,  $R > 0.50$  implies overlapping, but clearly different groups, and  $R < 0.25$  indicates that groups are barely separable (Clarke & Gorley, 2006). The associated  $p$ -values provide statistical confirmation that the samples within groups are more similar than can be expected by chance. ANOSIM was used to confirm whether the cluster patterns identified in the dendrogram and ordination were statistically significant.

The number of species unique to each habitat, shared between two habitats, and common to all three habitats, was illustrated in a Venn diagram. Dissimilarity between habitats was assessed using the Jaccard index of similarity based on shared species presence-absence data (Magurran, 2004). The Jaccard index was calculated as:

$$C_j = j / (a + b - j)$$

where  $j$  is the number of species present in both habitats,  $a$  is the number of species in habitat A and  $b$  is the number of species in habitat B.

Beta diversity, or turnover, relates to species identities and how they change across a gradient (Whittaker, 1975), and is therefore a different measure to alpha diversity or local species richness (Gray, 2000). The beta diversity measure  $\beta_{sim}$  was chosen as a qualitative measure of species turnover, because it is suited to situations where there are large differences in species richness counts between sites (Magurran, 2004). This is because  $\beta_{sim}$  is based on actual compositional differences (species gains and losses) between assemblages, and is not influenced by local species richness gradients (Lennon *et al.*, 2001; Koleff *et al.*, 2003).  $\beta_{sim}$  was used to compare species turnover within and between habitats, based on pooled species presence-absence data for all taxa combined. To calculate  $\beta_{sim}$ ,  $a$  (the number of species common to both habitats),  $b$  (the number of species present in the neighbouring habitat, but not in the focal habitat, *i.e.* species gain) and  $c$  (the number of species present in the focal habitat, but not in the neighbouring habitat, *i.e.* species loss) were first calculated for each pair of sites. The original  $\beta_{sim}$  equation (Lennon *et al.*, 2001) was re-expressed by Koleff *et al.* (2003) in terms of these matching/mis-matching components ( $a$ ,  $b$  and  $c$ ) as:

$$\beta_{\text{sim}} = (\min(b, c) / (\min(b, c) + a))$$

Using the smaller value of  $b$  or  $c$  in the denominator reduces the impact of large differences in species richness (Magurran, 2004). Mean species turnover was calculated for each habitat and between pairs of habitats, and differences tested for using Kruskal-Wallis ANOVA.

Spatial autocorrelation was used to determine whether distance had any significant effect on beta diversity among sites and habitats. Spatial autocorrelation is the correlation between pairs of sites separated by a (spatial) distance (Legendre, 1993). Spatial autocorrelation should not be ignored or discounted, because it can produce misleading results in analyses of ecological patterns, that lead to inflated Type I errors (falsely rejecting the null hypothesis of no effect) (Lennon, 2000; Diniz-Filho *et al.*, 2003; Dormann *et al.*, 2007). Most spatial data in ecology show positive autocorrelation, especially in short distance classes, since sites in close proximity are often more similar to each other than expected by chance (Diniz-Filho *et al.*, 2003).

Spatial autocorrelation in the invertebrate assemblage composition among habitats (*i.e.* for all 23 sites), and within each of the three habitats, was examined using Mantel tests and Mantel correlograms (Legendre & Legendre, 1998), using SAM (Spatial Analysis in Macroecology version 4.0, Rangel *et al.*, 2006; 2010). Mantel tests were used to compare two matrices: a matrix of the Jaccard distance in assemblage composition of sites, calculated from species presence-absence data, and a matrix of the geographical distance between sites, measured in kilometres. The Mantel Z-statistic (*i.e.* matrix correlation) tests the statistical significance of the relationship between the matrices for each distance class, and is related to Pearson's correlation coefficient. Significance of autocorrelation statistics was tested using Monte Carlo permutation tests (999 randomisations) in SAM. Mantel test autocorrelation coefficients range from -1 to +1, with positive coefficients indicating positive spatial autocorrelation (*i.e.* sites close together have very similar species composition), and negative coefficients indicating negative spatial autocorrelation (*i.e.* sites close together have very different species composition) (Legendre & Legendre, 1998). Under the null hypothesis of no spatial autocorrelation, autocorrelation coefficients have an expected value close to zero. Mantel correlograms were constructed for the default number of distance classes, using equal numbers of pairwise comparisons in each distance class. A correlogram plots the relationship between autocorrelated values (in this case, Mantel  $r$  values) on the  $y$ -axis and separate distance classes among sites on the  $x$ -axis (Legendre & Legendre, 1998). Correlograms can be plotted for single variables, such as species richness, using Moran's  $I$ , or for multivariate data, such as assemblage composition, using Mantel tests (Legendre & Legendre, 1998).

#### *Cape Peninsula endemic invertebrate species analyses*

The total and mean ( $\pm$  SD) numbers of Cape Peninsula endemic invertebrate species were tallied, and the numbers of endemic species per site plotted. Mean numbers of endemic species per site were compared using Kruskal-Wallis tests. Dissimilarity in the number of endemic species between habitats was assessed using the Jaccard index of similarity based on shared endemic species presence-absence data.

#### *Alien invertebrate species analyses*

The total and mean ( $\pm$  SD) numbers of alien invertebrate species were tallied, and the mean numbers of alien species per site plotted. Mean numbers of alien species per site were compared using Kruskal-Wallis tests. Dissimilarity in the number of alien species between habitats was assessed using the Jaccard index of similarity based on shared alien species presence-absence data. The percentage contribution of alien species to the number of individuals in each habitat, to the total and mean numbers of species in each habitat, and to the cumulative total number of species collected, was calculated. The percentage contribution of alien species to the total number of species and individuals collected in each habitat was also calculated for each group of alien invertebrates.

## **Results**

#### *Species richness and abundance*

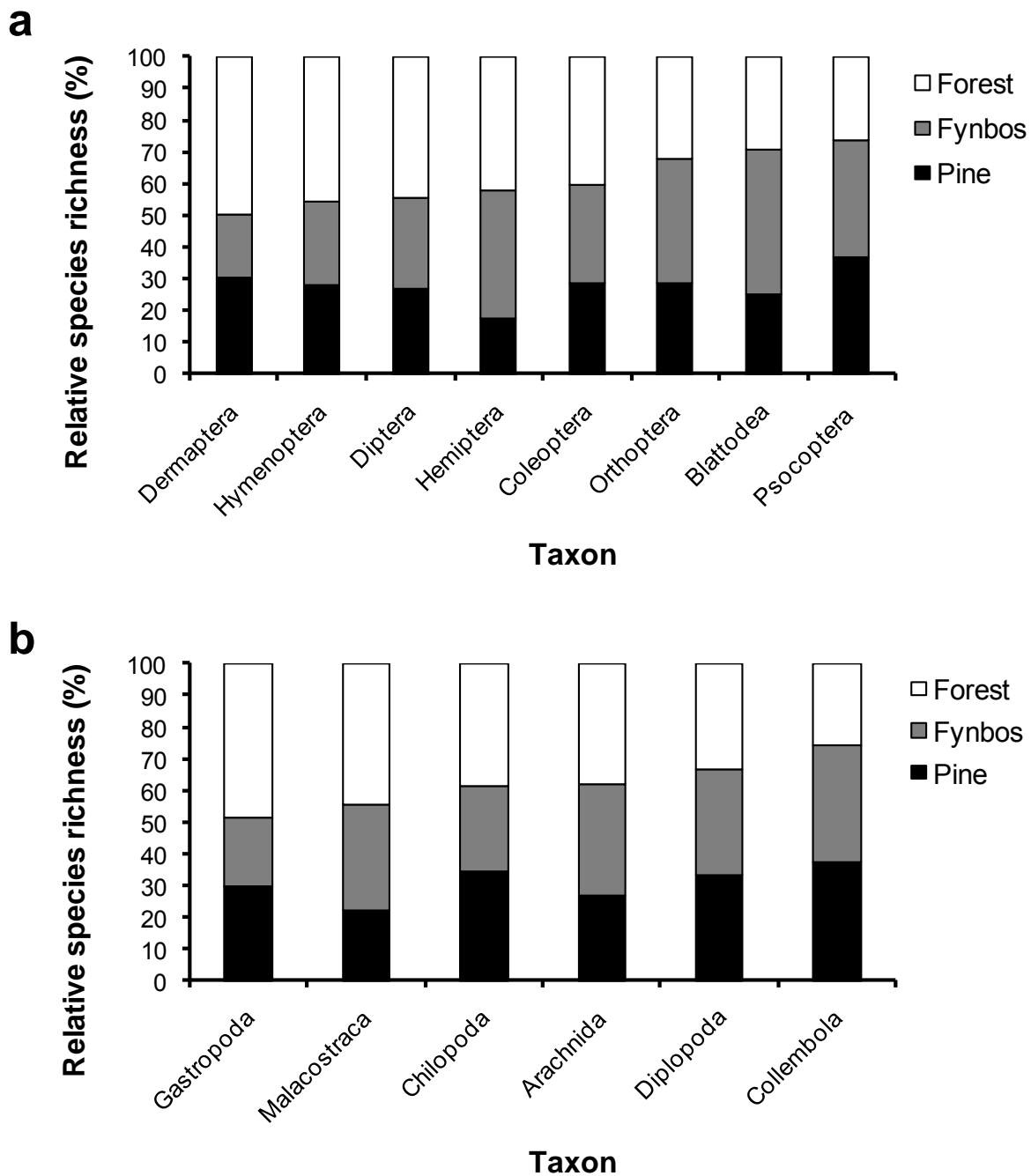
A raw total of 92 109 individuals from 670 species was collected from the 23 sites sampled (Table 3.1). These species spanned five invertebrate phyla (Annelida, Arthropoda, Mollusca, Onychophora and Platyhelminthes), 10 classes and 38 orders. Observed species richness ranged from 132-180 species per site in forest, from 65-118 in fynbos and from 83-135 in pine plantation. Total observed species richness was lower in pine plantation (311 species) than in either forest (455) or fynbos (365). Total abundance was also lower in pine plantation (19 614 individuals) than in either forest (38 131) or fynbos (34 364).

Relative observed species richness was lowest in pine plantation for most insect orders (Fig. 3.1a). Relative observed species richness in each habitat varied among non-insect classes, but was never highest in pine plantation (Fig. 3.1b). Relative abundance in each habitat varied among insect orders (Fig. 3.2a). Of the three insect orders most abundant in forest (Lepidoptera, Archaeognatha and Dermaptera), only Dermaptera was also abundant in pine

plantation. The three most abundant insect orders in fynbos were Blattodea, Hymenoptera and Orthoptera. Hemiptera and Psocoptera were numerically dominant in pine plantation, and appear to be tolerant of this exotic monoculture. Coleoptera and Diptera had similar abundances in each habitat, suggesting that these Orders include both forest and fynbos specialists, and many widespread generalist species. Mantodea, Neuroptera, Phasmatodea, Thysanoptera and Thysanura were discounted from comparisons, because each was represented by very few individuals and only one or two species. The abundance of all non-insect classes was highest in forest and lowest in fynbos (Fig. 3.2b), while Malacostraca had similar numbers in fynbos and pine plantation.

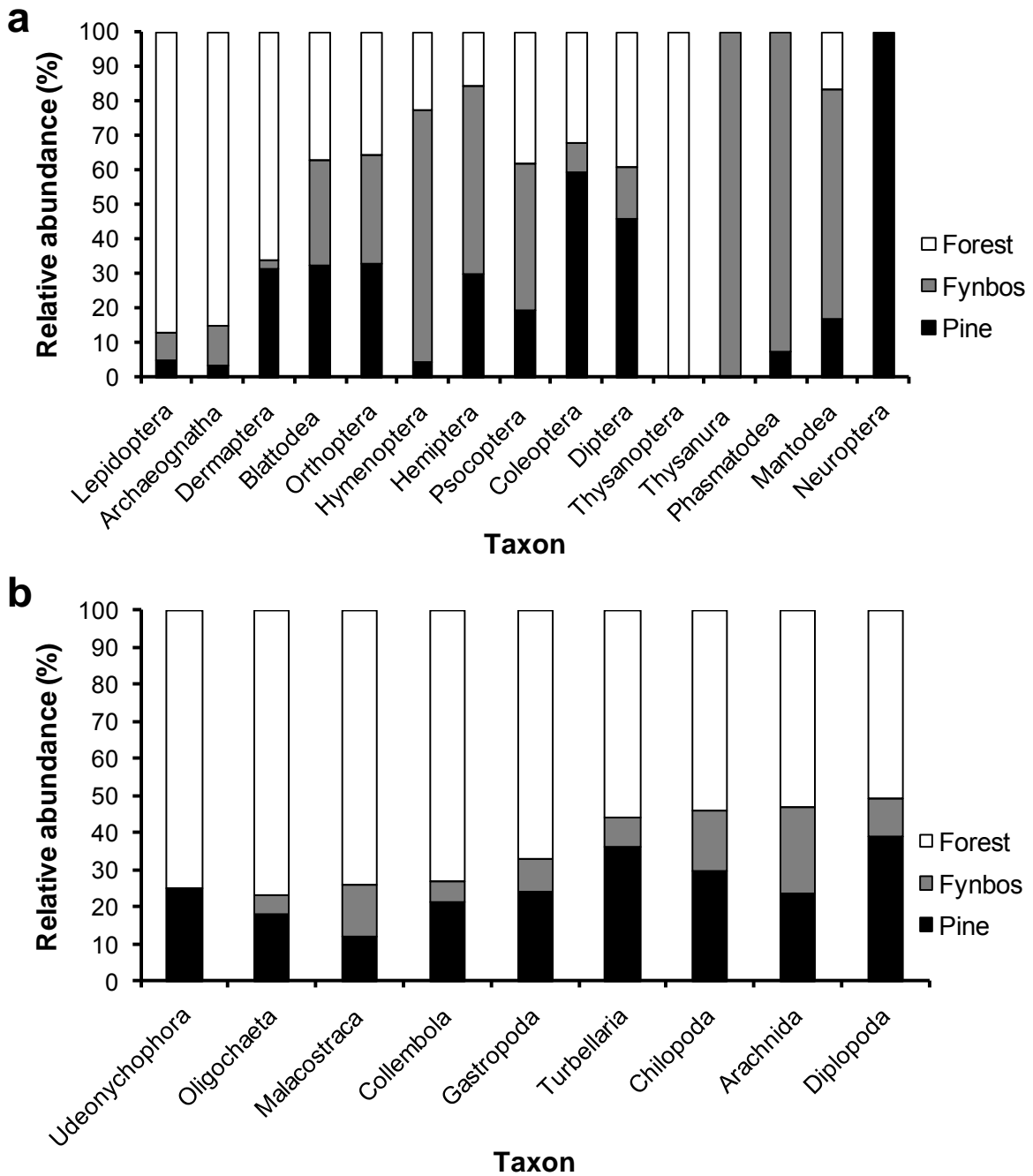
**Table 3.1.** Raw total species richness (number of species) and abundance (number of individuals) of invertebrate taxa collected in each habitat, with the number of species unique to each habitat in parentheses.

Common name	Taxon	Species richness				Abundance		
		Total	Forest	Fynbos	Pine	Forest	Fynbos	Pine
Ants	Formicidae	17	11	17 (4)	12	26 819	29 878	13 546
Bees	Hymenoptera	3	0	3 (3)	0	0	5	0
Beetles	Coleoptera	135	98 (34)	75 (17)	69 (12)	1401	1174	1221
Bristletails	Thysanura	1	1	1	1	167	22	7
Bugs	Hemiptera	75	46 (24)	44 (21)	19 (4)	454	123	843
Centipedes	Chilopoda	11	10	7	9 (1)	134	40	74
Cockroaches	Blattodea	12	7	11 (4)	6 (1)	122	397	24
Crickets	Orthoptera	15	9 (1)	11 (5)	8	154	532	290
Earthworms	Oligochaeta	1	1	1	1	1113	75	263
Earwigs	Dermaptera	5	5 (1)	2	3	135	5	64
Bristletails	Archaeognatha	1	0	1 (1)	0	0	4	0
Flatworms	Turbellaria	1	1	1	1	34	5	22
Flies	Diptera	70	43 (25)	28 (12)	26 (12)	714	630	658
Harvestmen	Opiliones	7	7 (2)	5	5	811	50	101
Lacewings	Neuroptera	1	0	0	1 (1)	0	0	1
Landhoppers	Amphipoda	2	2	2	2	1619	168	235
Millipedes	Diplopoda	10	8 (1)	8	8	852	169	649
Mites	Acari	17	14 (2)	10	15 (2)	359	249	374
Moths	Lepidoptera	1	1	1	1	151	14	8
Praying mantids	Mantodea	2	1	1 (1)	1	1	4	1
Pseudoscorpions	Pseudoscorpiones	5	4 (1)	2	3 (1)	28	14	8
Psocids/barklice	Psocoptera	11	5 (1)	7 (2)	7 (2)	47	18	55
Scorpions	Scorpiones	2	1	2	2	9	22	7
Slugs	Gastropoda	4	4 (1)	3	3	166	37	157
Snails	Gastropoda	16	14 (7)	5 (1)	8 (1)	527	54	91
Spiders	Araneae	106	68 (24)	67 (28)	41 (4)	215	280	138
Springtails	Collembola	19	9	13 (4)	13 (4)	1528	121	444
Stick insects	Phasmatodea	2	0	2 (1)	1	0	13	1
Sun-spiders	Solifugae	1	0	1 (1)	0	0	7	0
Thrips	Thysanoptera	1	1 (1)	0	0	2	0	0
Velvet worms	Udeonychophora	1	1	0	1	6	0	2
Wasps	Hymenoptera	108	77 (48)	30 (14)	42 (14)	380	85	269
Woodlice	Isopoda	7	6 (3)	4 (1)	2	183	169	61
	<b>Total</b>	<b>670</b>	<b>455 (176)</b>	<b>365 (120)</b>	<b>311 (59)</b>	<b>38 131</b>	<b>34 364</b>	<b>19 614</b>



**Figure 3.1.** Relative observed species richness in each habitat, expressed as a percentage of the total species in each taxon for (a) insect orders and (b) non-insect classes. Taxa represented by only one or two species (Archaeognatha, Mantodea, Neuroptera, Phasmatodea, Thysanoptera, Thysanura, Turbellaria and Udeonychophora) and unidentified taxa (Lepidoptera and Clitellata) are omitted.

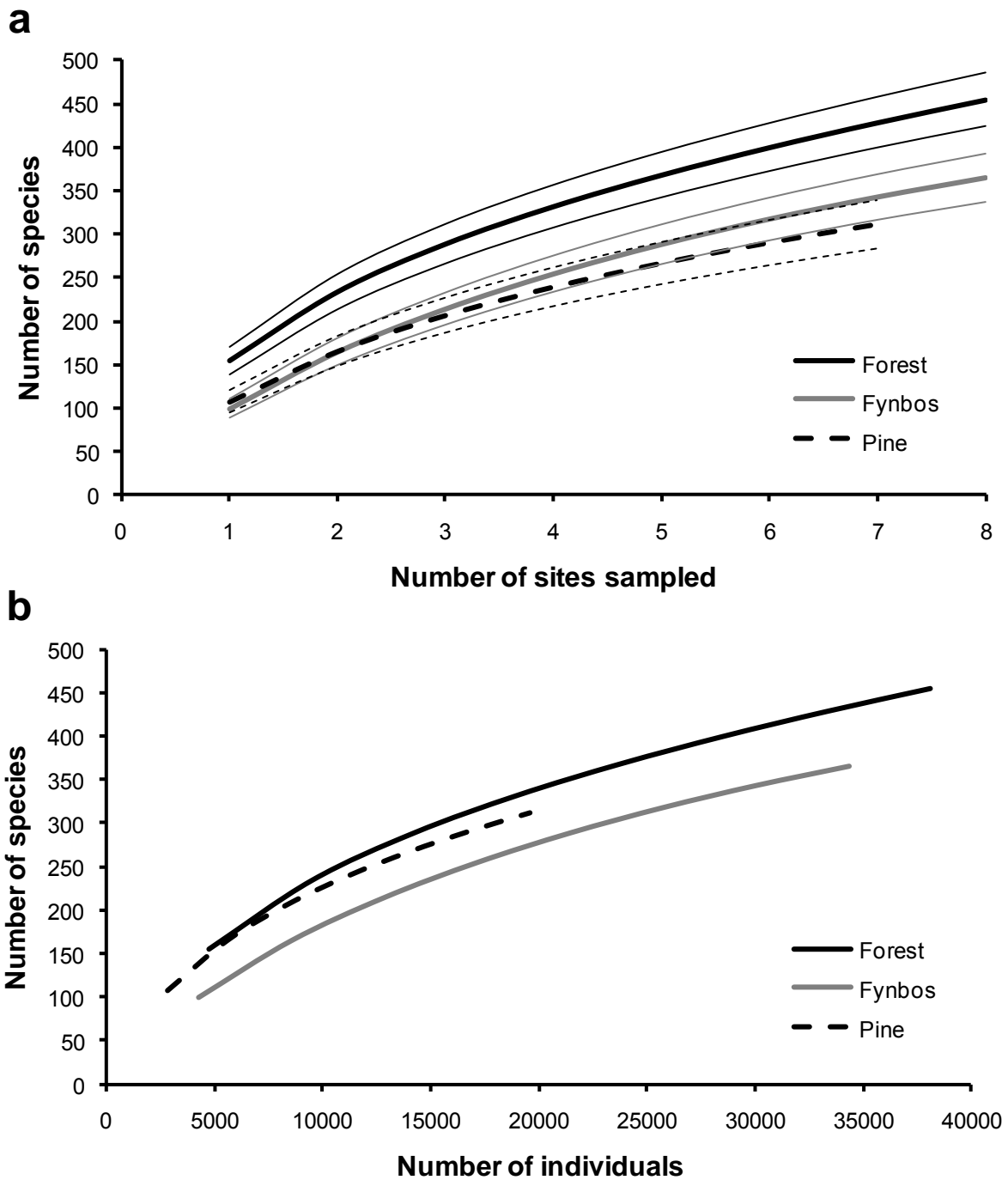




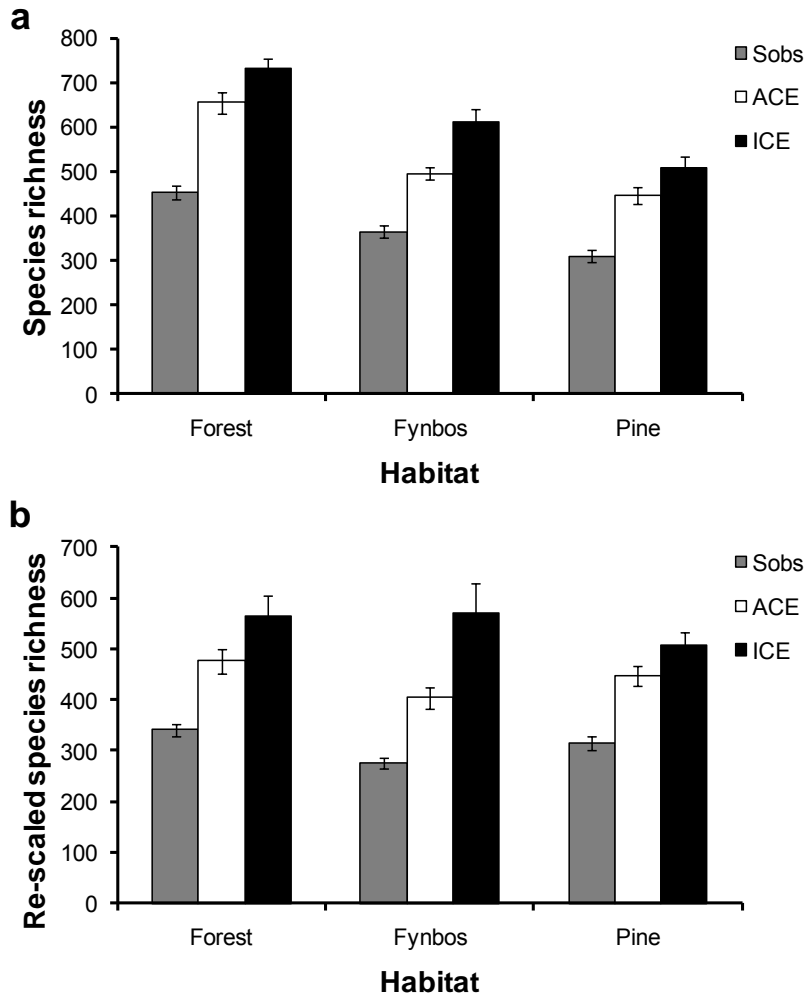
**Figure 3.2.** Relative abundance in each habitat, expressed as a percentage of the total abundance in each taxon for (a) insect orders and (b) non-insect classes.

Sample-based cumulative observed species richness was lower in pine plantation ( $311 \pm 14.0$  SD species) than in both forest ( $455 \pm 15.5$ ) and fynbos ( $365 \pm 14.3$ ). Sampling, as expected, approached, but did not achieve, saturation (Fig. 3.3a). Re-scaling of the x-axis of sample-based rarefaction curves from sites sampled to individuals (Fig. 3.3b) retained forest as the habitat with the highest observed species richness. However, an abundance-standardised comparison of 19 614 individuals (based on the lowest total abundance, recorded in pine plantation) suggests that the true species richness in pine plantation is in fact closer to that in forest, and not to fynbos.

Since accumulation curves did not reach an asymptote, estimated species richness was higher than observed species richness in all three habitats for both species richness estimators used (Fig. 3.4a). Estimated species richness based on incidence (ICE) was higher in all habitats than when based on abundance (ACE), which is not unexpected in patchy (heterogeneous) environments. After abundance-standardisation, observed and estimated species richness means were lower in both forest and fynbos, but unchanged in pine plantation (Fig. 3.4b). The abundance-standardised  $S_{\text{obs}}$  and ACE mean species richness were lower in fynbos than in pine plantation. The trend of the lowest estimated species richness based on ICE recorded in pine plantation remained unchanged.



**Figure 3.3.** Sample-based rarefaction curves of observed species richness in forest, fynbos and pine plantation with (a) number of sites sampled and (b) number of individuals. Curves were calculated using  $S_{obs}$  Mao Tau and randomised 50 times. Since curves did not reach an asymptote, and the 95% confidence intervals (thin lines) for fynbos and pine overlapped, the sample-based rarefaction curves were re-scaled to number of individuals.



**Figure 3.4.** Mean  $\pm$  SD observed species richness ( $S_{obs}$  Mao Tau) and estimated species richness based on abundance (ACE) and incidence (ICE) from sample-based rarefaction curves (a) of sites sampled and (b) after re-scaling to individuals (*i.e.* abundance-standardised curves).

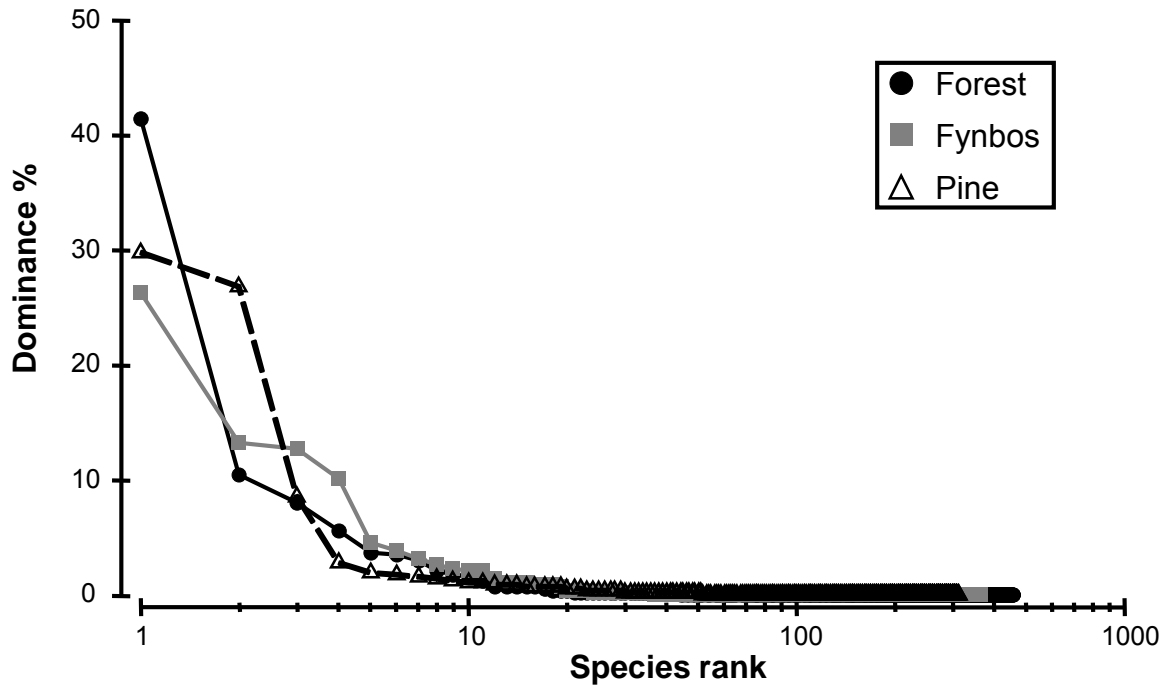
Species richness was 1.4-1.5 times higher in forest than in pine plantation, 1.2-1.3 times higher in forest than in fynbos, and 1.1-1.2 times higher in fynbos than in pine plantation (Table 3.2). Ratios varied marginally between observed and estimated species richness, and among estimators. Nevertheless, the pattern of highest species richness in forest persisted across all estimators. After abundance-standardisation (re-scaling to individuals), forest was only 1.1 times richer than pine plantation, but fynbos was no longer richer than pine plantation for either observed species richness or estimated species richness based on abundance (ACE).

**Table 3.2.** Ratios of sample-based observed species richness ( $S_{\text{obs}}$ ) and estimated species richness based on abundance (ACE) and incidence (ICE).

Comparison	Sample-based species richness			Rescaled to individuals		
	$S_{\text{obs}}$	ACE	ICE	$S_{\text{obs}}$	ACE	ICE
Forest / Pine	1.5	1.5	1.4	1.1	1.1	1.1
Fynbos / Pine	1.2	1.1	1.2	0.9	0.9	1.1
Forest / Fynbos	1.2	1.3	1.2	1.2	1.2	1.0

Mean sample-based observed species richness per site was higher in forest ( $154.6 \pm 16.3$  SD species,  $n = 8$ ) than in both fynbos ( $99.9 \pm 16.7$ ,  $n = 8$ ) and pine plantation ( $107.9 \pm 20.6$ ,  $n = 7$ ). Mean abundance-standardised species richness per site was still higher in forest ( $83.1 \pm 26.1$  SD species,  $n = 7$ ) than in both fynbos ( $59.7 \pm 30.5$ ,  $n = 7$ ) and pine plantation ( $69.7 \pm 19.0$ ,  $n = 7$ ). ANOVA showed a highly significant difference ( $F = 21.693$ ,  $df = 2$ ,  $p < 0.001$ ) between forest, fynbos and pine plantation sample-based observed species richness. A Kolmogorov-Smirnov test confirmed that the residuals were normally distributed ( $p = 0.936$ ), and a Levene's test confirmed that the variance of the residuals was equal among the three habitats ( $F = 0.855$ ,  $df = 2$ ,  $p = 0.440$ ). Tukey HSD for unequal  $N$  post hoc tests showed that the species richness of forest differed significantly from that of fynbos and pine plantation ( $p < 0.001$ ), but fynbos and pine plantation did not differ significantly in sample-based observed species richness ( $p = 0.668$ ). This confirms the patterns of observed and estimated species richness (Figs 3.3a and 3.4a). ANOVA of abundance-standardised species richness showed no significant difference among habitats ( $p = 0.256$ ). Mean abundance per site was lower in pine plantation ( $2802.0 \pm 1063.6$  SD individuals) than in forest ( $4766.4 \pm 3005.3$ ) and fynbos ( $4295.5 \pm 2432.1$ ), although these differences were not significant (Kruskal-Wallis  $H_{(N=23)} = 2.526$ ,  $df = 2$ ,  $p = 0.283$ ) due to the high variance among sites within each habitat.

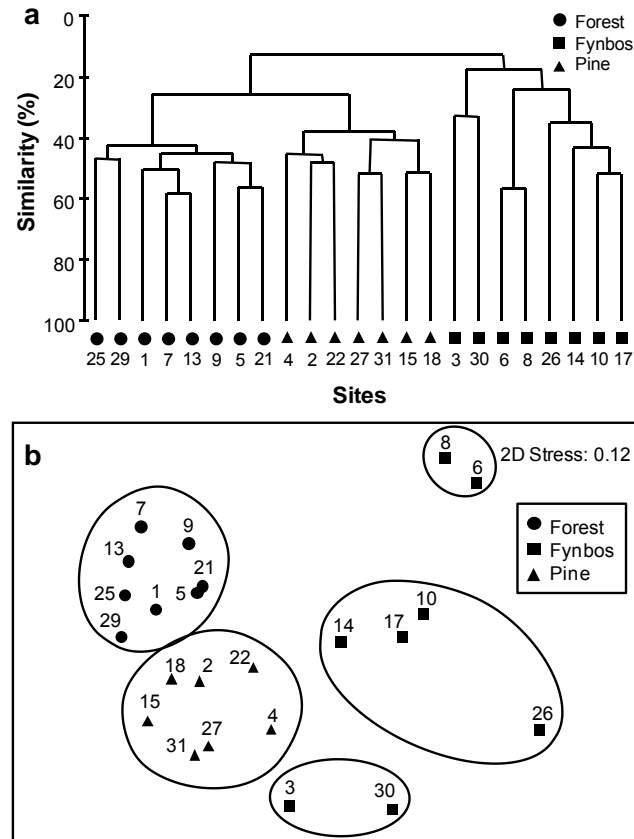
Very few common (*i.e.* highly abundant) species were recorded in each habitat, and most species were rare, represented by only a few individuals (Fig. 3.5). Species evenness was low in all habitats and only a few high ranking species had very high abundance. Dominance was higher for the highest ranking species in forest than in fynbos and pine plantation, but was similar for lower ranking species, suggesting that there is not greater dominance in one habitat.



**Figure 3.5.** Species-rank abundance curves (x-axis logged) for each habitat to compare dominance among habitats.

#### *Community composition and species turnover*

Invertebrate community composition differed among sites within habitats, and among habitats (forest, fynbos and pine plantation). However, sites clustered into distinct groups according to habitat, with low (15-25%) similarity among habitats, and with forest and pine plantation communities more similar to each other than to fynbos (Fig. 3.6a). Similarly, the MDS plot (Fig. 3.6b) showed forest and pine plantation sites clustered in two distinct groups close to, but not overlapping, each other. Fynbos sites separated from forest and pine plantation on the x-axis, but showed little similarity to one another, separating out across the y-axis into three clusters: Granite Fynbos (Sites 6 and 8), Sandstone Fynbos (Sites 10, 14, 17 and 26) and recovering Sandstone Fynbos that was previously under pine (Sites 3 and 30).

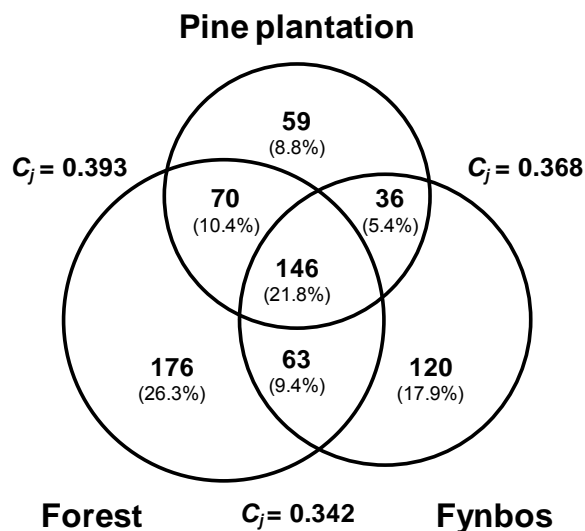


**Figure 3.6.** (a) Cluster analysis and (b) ordination from non-metric multidimensional scaling (MDS) applied to a Bray-Curtis dissimilarity matrix of log-transformed invertebrate community composition amongst sites. Numbers refer to sites (see Appendix A) and symbols to habitats. Clusters on the MDS ordination reflect 25% similarity among sites.

ANOSIM confirmed that community composition differed significantly among habitats. Forest community composition differed the most compared to pine plantation ( $R = 0.927$ ,  $p = 0.001$ ) and fynbos ( $R = 0.768$ ,  $p = 0.001$ ), with the least (although still highly significant) difference between fynbos and pine plantation habitats ( $R = 0.589$ ,  $p = 0.001$ ), as seen in the MDS ordination. An  $R$ -value of 0.589 (between fynbos and pine plantation) suggests overlapping, although clearly different groups of sites. With the exclusion of the two recovering Sandstone Fynbos sites (Sites 3 and 30) that were previously under pine, all pairwise habitat combinations showed well separated groups of sites: forest-pine plantation ( $R = 0.920$ ,  $p = 0.001$ ), forest-fynbos ( $R = 0.923$ ,  $p = 0.001$ ) and fynbos-pine plantation ( $R = 0.823$ ,  $p = 0.002$ ).

Over half (355) of the 670 species collected were found in one habitat only, while 146 (21.8%) were common to all three habitats sampled (Fig. 3.7). The number of species shared

only between forest and pine plantation (70) was almost double the number shared only between fynbos and pine plantation (36). Forest and pine plantation shared the highest number of species in total (216, or 32.2% of the 670 collected), and had the highest Jaccard index of similarity ( $C_j = 0.393$ ). Pine plantation supported considerably fewer unique species (59) than either forest (176) or fynbos (120). In forest, 103 of the 176 unique species were represented by only one individual (singletons) and 24 by two individuals (doubletons). In fynbos, 55 of the 120 unique species were singletons and 24 were doubletons. In pine plantation, 43 of the 59 unique species were singletons and 4 were doubletons. When expressed as a percentage of the total number of species collected in each habitat, singletons contributed a lower percentage in pine plantation (13.8% of the 311 species) than in both forest (22.6% of 455) and fynbos (15.1% of 365). Similarly, doubletons contributed a lower percentage in pine plantation (1.3% of the 311 species) than in both forest (5.3% of 455) and fynbos (6.6% of 365). Many of these unique species were collected from one site only: 124 species in forest (70.5%), 76 in fynbos (63.3%) and 51 in pine plantation (86.4%). Snails, spiders, bugs, beetles, flies and wasps contributed the highest number of unique species in all habitats (Table 3.1).

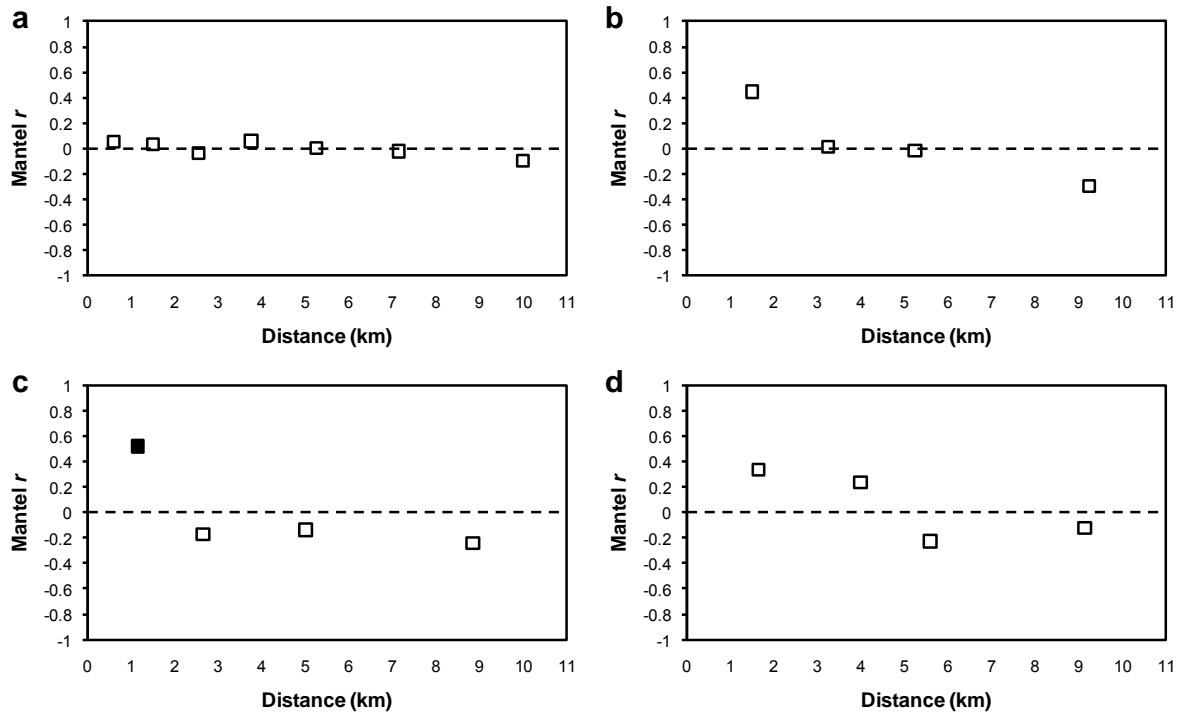


**Figure 3.7.** Venn diagram illustrating the number of unique species in each habitat and the number shared between habitats. The number of species is also expressed as a percentage of the total 670 species (values in parentheses). The Jaccard index of similarity ( $C_j$ ) is shown between each pair of habitats.



Species turnover or beta diversity, calculated as  $\beta_{\text{sim}}$ , was high and differed significantly both within habitats (Kruskal-Wallis  $H_{(N=77)} = 23.825$ ,  $df = 2$ ,  $p < 0.001$ ) and between habitats (Kruskal-Wallis  $H_{(N=176)} = 69.462$ ,  $df = 2$ ,  $p < 0.001$ ). Mean species turnover within habitats was slightly lower in pine plantation ( $0.473 \pm 0.058$  SD,  $n = 21$ ) than in forest ( $0.522 \pm 0.115$ ,  $n = 28$ ) and fynbos ( $0.611 \pm 0.078$ ,  $n = 28$ ). Mean species turnover between habitats was also slightly lower between forest and pine ( $0.527 \pm 0.068$  SD,  $n = 56$ ) than between forest and fynbos ( $0.646 \pm 0.072$ ,  $n = 64$ ) and between fynbos and pine ( $0.652 \pm 0.077$ ,  $n = 56$ ). The high mean turnover between habitats reflects the contrasting invertebrate assemblages present in each habitat. The furthest distance between any two sites was less than 12 km, which may be too close to show any meaningful trend in species turnover with distance. Factors such as site-specific environmental conditions, disturbance history and vegetation composition may have stronger influences on species turnover at this localized spatial scale.

As expected, no significant spatial autocorrelation among habitats was detected, with  $p > 0.05$  for all distance classes (Fig. 3.8a). Positive, but not significant ( $r = 0.448$ ,  $p = 0.069$ ) spatial autocorrelation was recorded at the shortest distance (1.5 km) in forest (Fig. 3.8b). Weak negative, but not significant ( $r = -0.295$ ,  $p = 0.248$ ) autocorrelation was recorded at the furthest distance class (9.25 km) in forest, with no autocorrelation at middle distance classes in forest (Fig. 3.8b). Similar patterns of spatial autocorrelation were recorded in fynbos (Fig. 3.8c), with significant positive autocorrelation ( $r = 0.519$ ,  $p = 0.006$ ) at the shortest distance (1.15 km). Interestingly, the shortest distance class in fynbos was the only significantly autocorrelated distance class either among habitats (Fig. 3.8a), or within habitats (Fig. 3.8b-d). Although not significant, positive autocorrelation at the two short distance classes ( $r = 0.333$ ,  $p = 0.135$  at 1.65 km and  $r = 0.235$ ,  $p = 0.262$  at 4 km) and weak negative autocorrelation at the two long distance classes ( $r = -0.226$ ,  $p = 0.298$  at 5.6 km and  $r = -0.125$ ,  $p = 0.632$  at 9.15 km), was recorded in pine plantation (Fig. 3.8d). In pine plantation, the most negative autocorrelation was not at the longest distance class. This may reflect a break between pine plantations at Cecilia Plantation on Table Mountain and Tokai Plantation on Silvermine Mountain, as the two mountains are separated by Orange Kloof valley.



**Figure 3.8.** Mantel correlograms showing spatial autocorrelation in invertebrate assemblage composition among sites across distance classes (a) among habitats and within (b) forest, (c) fynbos and (d) pine plantation. Distance classes were determined by equal number of site pair comparisons. The dark square symbol in (c) represents the only distance class for which the Mantel test was significant ( $p \leq 0.05$ ).

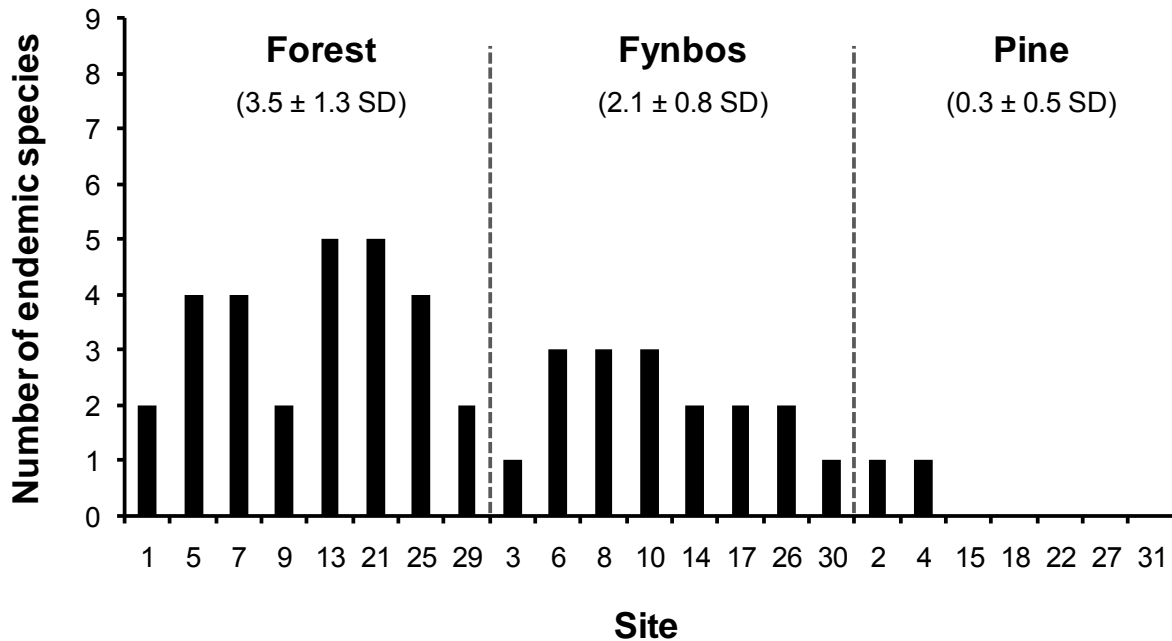
#### *Cape Peninsula endemic invertebrates*

Nine species were identified by taxonomists as Cape Peninsula endemics and/or were amongst those listed in Picker & Samways (1996) as being endemic to the Cape Peninsula (Table 3.3). Of these, seven were collected in forest, six in fynbos and only one (*Uroplectes insignis*) in pine plantation, although it also occurred in both native habitats. Three Cape Peninsula endemic species were unique to forest (*Trachycystis perplicata*, *Spermophora peninsulae* and *Bohepilissus nitidus*), and two to fynbos (*Dipteretrum brinckae* and *Hoplophoropyga unicolour*). Only one endemic species was shared across all three habitats, and no endemic species were shared between forest and pine plantation, or fynbos and pine plantation. Consequently, the Jaccard index of similarity was much higher between forest and fynbos ( $C_j = 0.444$ ) than between forest and pine plantation ( $C_j = 0.143$ ) or fynbos and pine plantation ( $C_j = 0.167$ ).

**Table 3.3.** Distribution of Cape Peninsula endemic invertebrate species by habitat. Total abundance (in bold), mean abundance per site ( $\pm$  SD) and number of sites (both in parentheses) are given for each species in each habitat.

Order	Endemic species	Forest	Fynbos	Pine
Eupulmonata	<i>Trachycystis perplicata</i> (Benson, 1851)	<b>6</b> (0.8 $\pm$ 1.4, n = 3)	<b>0</b>	<b>0</b>
Araneae	<i>Spermophora gordimerae</i> Huber, 2003	<b>6</b> (0.8 $\pm$ 1.8, n = 2)	<b>3</b> (0.4 $\pm$ 0.7, n = 2)	<b>0</b>
Araneae	<i>Spermophora peninsulae</i> Lawrence, 1964	<b>1</b> (0.1 $\pm$ 0.4, n = 1)	<b>0</b>	<b>0</b>
Araneae	<i>Malaika longipes</i> (Purcell, 1904)	<b>14</b> (1.8 $\pm$ 1.6, n = 6)	<b>2</b> (0.3 $\pm$ 0.7, n = 1)	<b>0</b>
Araneae	<i>Moggridgea teresae</i> Griswold, 1987	<b>8</b> (1.0 $\pm$ 1.1, n = 5)	<b>1</b> (0.1 $\pm$ 0.4, n = 1)	<b>0</b>
Scorpiones	<i>Uroplectes insignis</i> Pocock, 1890	<b>9</b> (1.1 $\pm$ 1.5, n = 4)	<b>13</b> (1.6 $\pm$ 2.4, n = 3)	<b>6</b> (0.9 $\pm$ 1.6, n = 2)
Blattodea	<i>Dipteretrum brinckae</i> Princis, 1963	<b>0</b>	<b>53</b> (6.6 $\pm$ 12.9, n = 5)	<b>0</b>
Blattodea	<i>Hoplophoropyga unicolor</i> (Karny, 1908)	<b>0</b>	<b>32</b> (4.0 $\pm$ 5.3, n = 5)	<b>0</b>
Coleoptera	<i>Bohepilissus nitidus</i> Balthasar, 1965	<b>115</b> (14.4 $\pm$ 26.3, n = 7)	<b>0</b>	<b>0</b>

None of the endemic species was collected at all sites within a habitat, and most were rare and only collected from a few sites. Only two of the seven pine plantation sites, both in Newlands Forest, supported the Cape Peninsula endemic scorpion *U. insignis*. Forest generally had the greatest number of endemic species per site (Fig. 3.9). The mean number of endemic species in forest ( $3.5 \pm 1.3$  SD species), fynbos ( $2.1 \pm 0.8$ ) and pine plantation ( $0.3 \pm 0.5$ ) was significantly different between habitats (Kruskal-Wallis  $H_{(N=23)} = 15.657$ ,  $df = 2$ ,  $p < 0.001$ ), reflecting the low number of endemic species recorded in pine plantation. Cape Peninsula endemic species made a very low percentage contribution (1.35% cumulatively) to the total 670 species collected.



**Figure 3.9.** Number of Cape Peninsula endemic invertebrate species collected at each site, with mean ( $\pm$  SD) number per habitat in parentheses.

#### *Alien invertebrates*

Nineteen alien invertebrate species were identified, of which 16 were collected in forest, 11 in fynbos and 15 in pine plantation (Table 3.4). Alien species contributed a slightly higher percentage to the total number of species collected in pine plantation (5.14% of the 311 species) than in both forest (3.30% of 455) and fynbos (3.01% of 365). Cumulatively, alien species contributed only 2.84% to the total 670 invertebrate species collected.

The total number of individual alien invertebrates was higher in forest (16 663 individuals) than in both fynbos (4865) and pine plantation (6657). Similarly, the percentage contribution of alien species to the total number of individuals in each habitat was higher in forest (43.7%) than in fynbos (14.1%) or pine plantation (33.94%). However, these numbers were strongly biased by the number of individual Argentine ants collected. With Argentine ants excluded, forest still had a higher number of aliens (834 individuals) than both fynbos (319) and pine plantation (816). However, pine plantation had almost double the percentage of non-ant individuals collected in each habitat: 13.45% compared to 7.37% in forest and 7.11% in fynbos.

The Jaccard index of similarity was higher between forest and pine plantation ( $C_j = 0.722$ ) than between forest and fynbos ( $C_j = 0.588$ ), or fynbos and pine plantation ( $C_j = 0.625$ ).

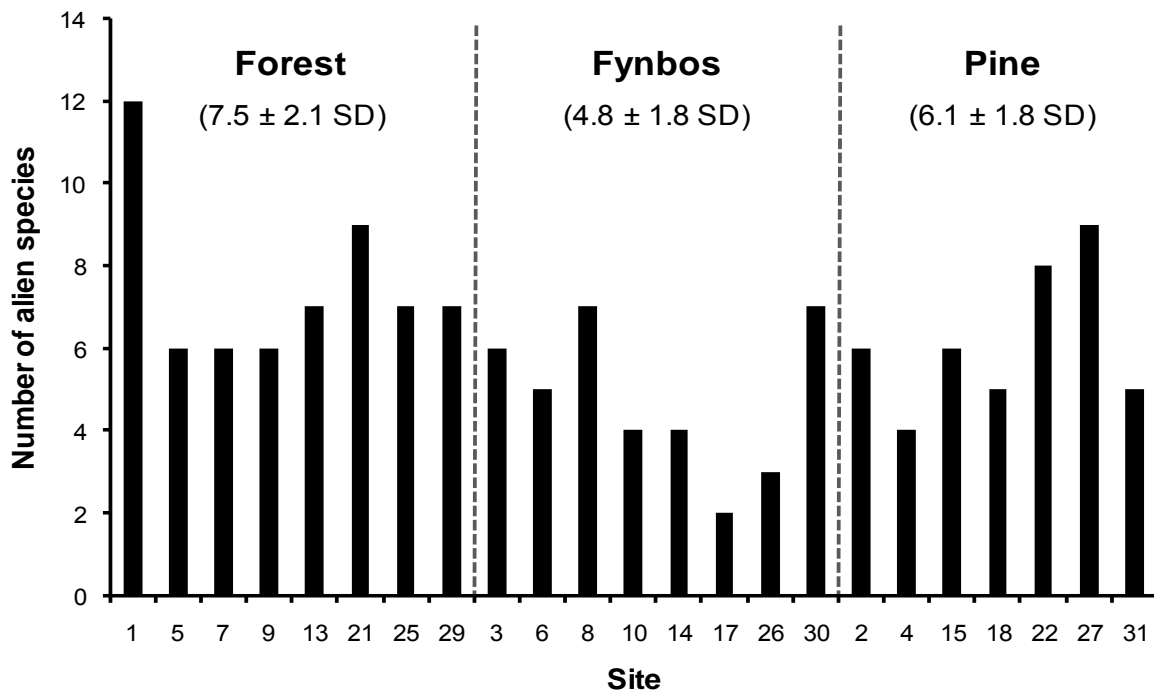
Over half of the alien species collected were present in all three habitats, with a further three species shared between forest and pine plantation. No alien invertebrate species was shared only between forest and fynbos, or only between fynbos and pine plantation. Three alien molluscs were found only in forest (*Limax maximus*, *Cochlicopa* sp. and *Cornu aspersum*); with the first two restricted to one site each (Table 3.4). One alien springtail (*Tomocerus minor*) was restricted to a single site in fynbos. An alien snail (*Lauria cylindracea*) and another alien springtail (*Entomobrya nivalis*) were each restricted to a single site in pine plantation. The alien Portuguese millipede (*Ommatoiulus moreleti*) was abundant in all 23 sites. *O. moreleti* was also far more abundant in all habitats than any of the native millipede species. An alien slug (*Arion hortensis*); although less abundant in fynbos, was present at 21 sites. The European wasp (*Vespula germanica*) was present in all habitats, although far less abundant in pine plantation than in forest or fynbos. The Argentine ant (*Linepithema humile*) was present at 16 of the 23 sites and in all three habitats.

Mean abundance per site of Argentine ants was higher in forest ( $1978.6 \pm 2571.1$  SD individuals) than in both fynbos ( $568.3 \pm 1277.6$ ) and pine plantation ( $834.4 \pm 1507.3$ ). Total abundance of Argentine ants was also higher in forest (15 829 individuals) than in either fynbos (4546) or pine plantation (5841), although these differences were not significant (Kruskal-Wallis  $H_{(N=23)} = 0.178$ ,  $df = 2$ ,  $p = 0.915$ ). The number of individual Argentine ants collected at each site varied greatly within habitats, with over 1000 individuals (suggesting a nest nearby) recorded in each of four forest, one fynbos and two pine plantation sites.

**Table 3.4.** Total abundance (in bold), mean  $\pm$  SD abundance per site and number of sites (in parentheses) for alien invertebrate species collected in each habitat.

Order: Family	Species	Forest	Fynbos	Pine
Eupulmonata: Arionidae	<i>Arion hortensis</i> aggregate Férussac, 1819	<b>106</b> (13.3 $\pm$ 8.1, n = 8)	<b>29</b> (3.6 $\pm$ 3.7, n = 7)	<b>131</b> (18.7 $\pm$ 23.4, n = 6)
Eupulmonata: Limacidae	<i>Deroceas panormitanum</i> (Lesson & Pollonera, 1882)	<b>30</b> (3.8 $\pm$ 5.5, n = 8)	<b>4</b> (0.5 $\pm$ 1.1, n = 2)	<b>3</b> (0.4 $\pm$ 1.1, n = 1)
Eupulmonata: Limacidae	<i>Lehmannia valentiana</i> (Férussac, 1821)	<b>28</b> (3.5 $\pm$ 3.0, n = 6)	<b>4</b> (0.5 $\pm$ 1.4, n = 1)	<b>23</b> (3.3 $\pm$ 5.8, n = 2)
Eupulmonata: Limacidae	<i>Limax maximus</i> Linnaeus, 1758	<b>2</b> (0.3 $\pm$ 0.7, n = 1)	<b>0</b>	<b>0</b>
Eupulmonata: Cochlicopidae	<i>Cochlicopa</i> sp. Férussac, 1821	<b>16</b> (2.0 $\pm$ 5.7, n = 1)	<b>0</b>	<b>0</b>
Eupulmonata: Cochlicopidae	<i>Cochlicopa</i> cf. <i>lubricella</i> Férussac, 1821	<b>56</b> (7.0 $\pm$ 19.8, n = 1)	<b>0</b>	<b>3</b> (0.4 $\pm$ 0.8, n = 2)
Eupulmonata: Pristilomatidae	<i>Vitrea contracta</i> (Westerlund, 1871)	<b>13</b> (1.6 $\pm$ 3.1, n = 2)	<b>0</b>	<b>19</b> (2.7 $\pm$ 5.5, n = 3)
Eupulmonata: Helicidae	<i>Cornu aspersum</i> (Müller, 1774)	<b>6</b> (0.8 $\pm$ 1.4, n = 3)	<b>0</b>	<b>0</b>
Eupulmonata: Punctidae	cf. <i>Punctum</i> sp.	<b>35</b> (4.4 $\pm$ 12.4, n = 1)	<b>0</b>	<b>38</b> (5.4 $\pm$ 5.5, n = 6)
Eupulmonata: Pupillidae	<i>Lauria cylindracea</i> (da Costa, 1778)	<b>0</b>	<b>0</b>	<b>1</b> (0.1 $\pm$ 0.4, n = 1)
Eupulmonata: Oxychilidae	<i>Oxychilus draparnaudi</i> (Beck, 1837)	<b>60</b> (7.5 $\pm$ 18.9, n = 3)	<b>2</b> (0.3 $\pm$ 0.7, n = 1)	<b>13</b> (1.9 $\pm$ 4.9, n = 1)
Eupulmonata: Oxychilidae	<i>Oxychilus</i> sp. Fitzinger, 1833	<b>9</b> (1.1 $\pm$ 2.4, n = 3)	<b>10</b> (1.3 $\pm$ 3.2, n = 2)	<b>10</b> (1.4 $\pm$ 3.4, n = 2)
Julida: Cambalidae	<i>Ommatoiulus moreleti</i> (Lucas, 1860)	<b>508</b> (63.5 $\pm$ 35.4, n = 8)	<b>152</b> (19.0 $\pm$ 25.6, n = 8)	<b>546</b> (78.0 $\pm$ 41.7, n = 7)
Isopoda: Porcellionidae	<i>Porcellio scaber</i> Latreille, 1804	<b>49</b> (6.1 $\pm$ 10.9, n = 6)	<b>99</b> (12.4 $\pm$ 27.2, n = 6)	<b>8</b> (1.1 $\pm$ 1.9, n = 3)
Collembola: Entomobryidae	<i>Entomobrya nivalis</i> (Linnaeus, 1758)	<b>0</b>	<b>0</b>	<b>16</b> (2.3 $\pm$ 6.0, n = 1)
Collembola: Neanuridae	<i>Neanura muscorum</i> (Templeton, 1835)	<b>1</b> (0.1 $\pm$ 0.4, n = 1)	<b>4</b> (0.5 $\pm$ 1.4, n = 1)	<b>2</b> (0.3 $\pm$ 0.5, n = 2)
Collembola: Tomoceridae	<i>Tomocerus minor</i> (Lubbock, 1862)	<b>0</b>	<b>1</b> (0.1 $\pm$ 0.4, n = 1)	<b>0</b>
Hymenoptera: Vespidae	<i>Vespula germanica</i> (Fabricius, 1793)	<b>15</b> (1.9 $\pm$ 3.6, n = 3)	<b>14</b> (1.8 $\pm$ 3.3, n = 2)	<b>3</b> (0.4 $\pm$ 0.8, n = 2)
Hymenoptera: Formicidae	<i>Linepithema humile</i> Mayr, 1868	<b>15 829</b> (1978.6 $\pm$ 2571.1, n = 5)	<b>4546</b> (568.3 $\pm$ 1277.6, n = 7)	<b>5841</b> (834.4 $\pm$ 1507.3, n = 4)

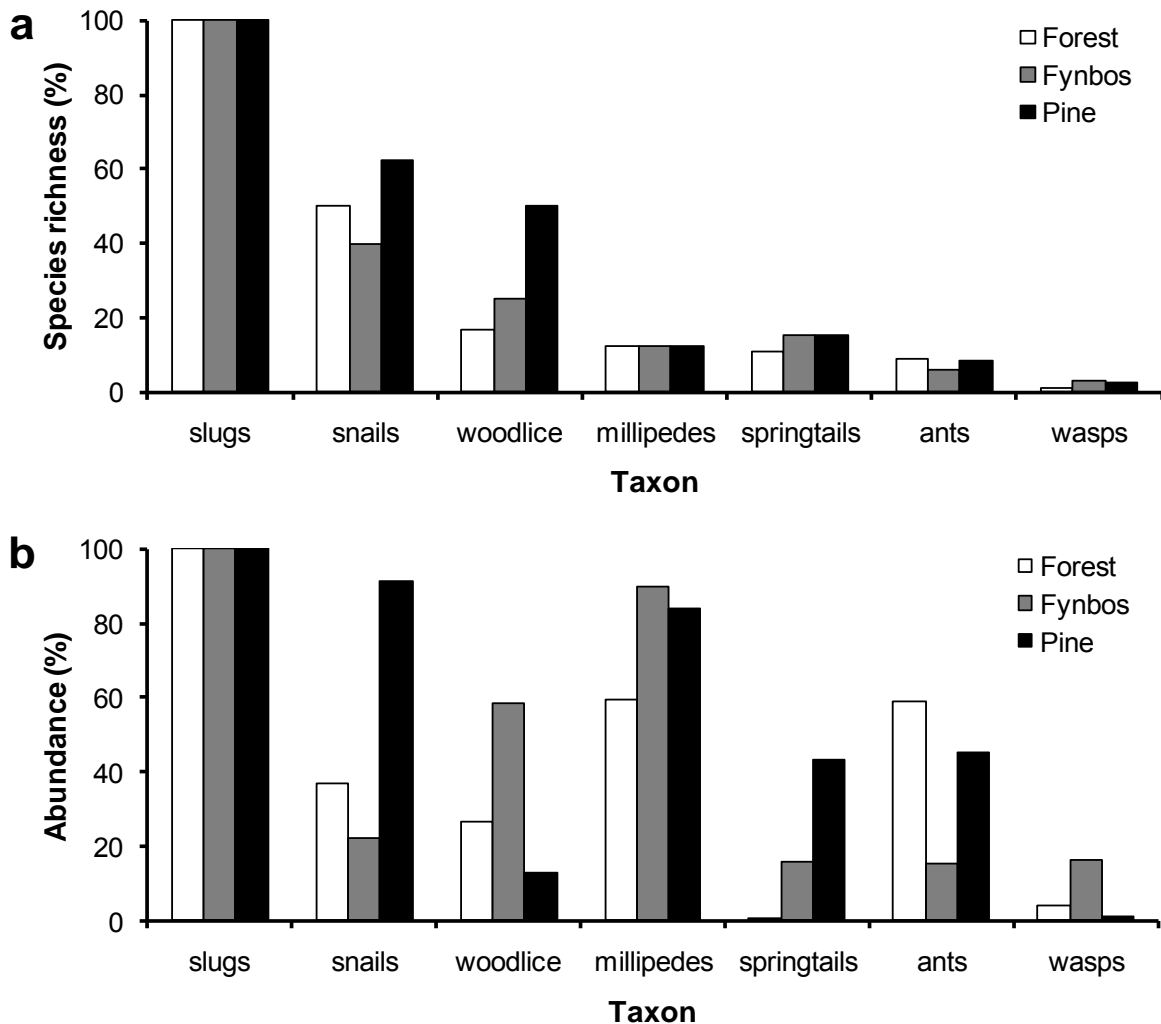
Every site harboured at least two alien species (Fig. 3.10). The highest number of alien species at any one site was 12 (Site 1, forest – in Newlands Forest) (Fig. 3.10). The mean number of alien species in forest ( $7.5 \pm 2.1$  SD species), fynbos ( $4.8 \pm 1.8$ ) and pine plantation ( $6.1 \pm 1.8$ ) was not significantly different between habitats (Kruskal-Wallis  $H_{(N=23)} = 6.215$ ,  $df = 2$ ,  $p = 0.447$ ). Alien species contributed a very low and similar percentage of the mean number of species collected per site in forest ( $4.86 \pm 1.19$  SD %), fynbos ( $4.78 \pm 1.78\%$ ) and pine plantation ( $5.80 \pm 1.80\%$ ).



**Figure 3.10.** Number of alien invertebrate species recorded at each site, with mean number ( $\pm$  SD) per habitat in parentheses.

The percentage contribution of alien species to the total number of species (Fig. 3.11a) and total number of individuals (Fig. 3.11b) collected in each habitat varied between taxa. The percentage contribution of alien species to the total number of species collected in each taxon in pine plantation was equal to, or higher than, that in both forest and fynbos (Fig. 3.11a). Snails and woodlice showed a higher percentage contribution of alien species in pine plantation than in native habitats. Alien species contributed only a small percentage of the species collected across habitats for most taxa, with the exception of molluscs, where all slug and half of the snail

species collected were alien. Trends differed between species richness and abundance. Several alien species were numerically dominant and made a disproportionately high contribution to the total number of individuals collected for slugs, snails and millipedes, especially in pine plantation (Fig. 3.11b).



**Figure 3.11.** Percentage contribution of alien taxa to the total (a) number of species and (b) number of individuals per taxon in each habitat.



## Discussion

### *Species richness and abundance*

Pine plantations on the Cape Peninsula supported a surprisingly rich ground-dwelling invertebrate assemblage, albeit less rich than that in surrounding native habitats (sample-based cumulative observed species richness of 311 species in pine plantation compared to 365 in fynbos and 455 in forest). However, this was not the case for abundance, which was approximately 50% lower in pine plantations compared to forest and fynbos. Nevertheless, species rank abundance curves suggest that species evenness is similarly very low in each habitat. Observed species richness was significantly lower in pine plantation than in forest, but not significantly lower than in fynbos, as was expected. According to Stephens & Wagner (2007), the worldwide literature reports generally lower biodiversity in plantations compared to natural forests (94% of studies), but relatively comparable richness compared to non-forested natural ecosystems (only 57% of studies report lower diversity in plantations). Re-scaling the x-axis of sample-based rarefaction curves suggests that the true species richness in pine plantation is closer to that in forest and higher than that in fynbos. With re-scaling for abundance-standardisation, estimated species richness patterns differed between ACE (abundance-based coverage estimator) and ICE (incidence-based coverage estimator), with ACE showing lower species richness in fynbos than in pine plantation. ICE performs well with moderate patchiness and small sample sizes (Magurran, 2004), but not when the number of rare species does not decrease with increased sampling effort (Colwell & Coddington, 1994). ACE may therefore offer a more reliable estimation of true species richness.

Fynbos supported comparatively low species richness. Fynbos is generally considered to support low diversity of ground-dwelling invertebrates (Giliomee, 2003), although quantitative, comparative studies are rare. Procheş & Cowling (2006) suggest that fynbos is not as insect-poor as previously thought, because previous generalisations were based on a handful of insect taxa, which appear to be under-represented in fynbos. In their comparative study of fynbos, grassland, thicket and karoo vegetation, Procheş & Cowling (2006) found that fynbos insect diversity was comparable to that of grassland and subtropical thicket, and richer than Nama-Karoo. This study is also not in agreement with previous findings of higher species richness in fynbos than in forest for epigeic invertebrates (147 species in fynbos and 123 in forest; Pryke & Samways, 2010) and aerial invertebrates (126 species in fynbos and 62 in forest; Pryke & Samways, 2008). Pryke & Samways' findings are likely to be artefacts of the high heterogeneity in fynbos vegetation types sampled around the Cape Peninsula. The present study attempted to

circumvent possible confounding abiotic and biotic heterogeneity in fynbos by controlling (as far as possible) for aspect, elevation and vegetation type. In both studies, Pryke & Samways also did not abundance-standardise data in their species rarefaction curves, which did not reach an asymptote in any habitat sampled for either taxon, so their richness findings may be misleading.

The low species richness observed in fynbos, compared to forest, may reflect the low cover, shallow depth of litter, and low soil and litter moisture levels found in summer in this habitat. Leaf litter depth and composition are known to affect abundance and assemblage composition of snails and other invertebrates (Martin & Sommer, 2004 and references therein), are often positively correlated with beetle diversity, and may be more important than soil moisture in explaining species richness patterns (Hopp *et al.*, 2010). The low rate of litter accumulation in fynbos has previously been used to explain the low number of soil and surface-dwelling invertebrates (Giliomee, 2003). Fynbos leaf litter production is affected by vegetation age (time since last fire) and the proportions of restioid, proteoid and ericoid species (Mitchell *et al.*, 1986). Fynbos litter also decomposes at a very slow rate (Mitchell *et al.*, 1986). Leaf litter is a highly specific microhabitat (Hopp *et al.*, 2010) and the fynbos leaf litter community has received insufficient attention in the literature and remains poorly understood. The results here suggest that fynbos is not as good a habitat as forest for litter-dwelling invertebrates, which is unsurprising, as forest litter is undoubtedly a superior habitat for this fauna. Fynbos litter may also represent a more transient habitat, given that fire frequency in fynbos would have occurred at 5-50 year intervals (Rebelo *et al.*, 2006), consuming much of the litter, albeit less frequently on Table Mountain. In contrast, forest is naturally protected from fire (Rebelo *et al.*, 2006) and thus offers a stable litter habitat in ecological and evolutionary time. Forest litter may also have greater input from the greater plant biomass compared to fynbos.

Contrary to prediction based on previous work done in the same area on litter invertebrates, species richness in pine plantations was not half that of Afrotropical forest. Forest was only 1.1 times richer than pine plantation after abundance-standardisation, compared to the 2.2 times (Raharinjanahary, 2007) and 2.4 times (Ratsirarson *et al.*, 2002) reported in earlier studies, and on which this prediction was based. Even before abundance-standardisation, forest was only 1.5 times richer than pine plantation in this study (Table 3.2). Interestingly, for the same sites sampled in Newlands Forest, the observed species richness was 1.3 times higher in forest than in pine plantation for both this study and Ratsirarson *et al.* (2002), despite the limited suite of taxa they sampled (Hymenoptera, Opiliones and Amphipoda) and their single sampling method (Winkler bag sifted leaf litter extractions). It was previously not known whether Newlands Forest, the only area sampled by Ratsirarson *et al.* (2002) and

Raharinjanahary (2007), is indeed representative of forest ground-dwelling invertebrate diversity patterns across the Cape Peninsula. Based on the present study, Newlands Forest does appear to be fairly representative (at least in forest and pine plantation), since invertebrate species richness estimates for the eight areas sampled across the Cape Peninsula suggest Afrotropical forests were 1.1 times richer than pine plantations after abundance-standardisation. However, species richness varied considerably across sites for all three habitats.

#### *Community composition and species turnover*

Species turnover, or beta diversity, was investigated using two complimentary approaches: a “raw data” approach of MDS ordination and ANOSIM, and a “distance” approach using the beta diversity index  $\beta_{sim}$  and Mantel tests of spatial autocorrelation. The “raw data” multivariate approach measures variation in community composition among sites, whereas the “distance” approach measures variation in beta diversity among groups (or pairs) of sites (Legendre *et al.*, 2005).

Community composition was significantly different in forest, fynbos and pine plantation, with 15-25% (circles on the MDS plot represent 25%) similarity among habitats. Distinct faunal assemblages associated with different habitats have been recorded in a range of forest/plantation habitats. Samways *et al.* (1996) found different invertebrate assemblages in exotic plantations (of various species) and invasive plants, compared to native woodland and grassland, with many species restricted to native vegetation, as was the case in this study. Lachat *et al.* (2006) found different arthropod communities in natural forest, young plantations and old plantations in Lama Forest reserve (South Benin), with the lowest species richness recorded in young plantations. Hopp *et al.* (2010) also found different litter-inhabiting beetle communities in young secondary and old-growth forests in the Atlantic Forest of Southern Brazil, suggesting that time since disturbance strongly influences community composition. Older plantation stands, like primary, old-growth forests, generally offer more spatial and vertical heterogeneity, better developed soil organic layers, and more accumulated litter and dead wood than young stands or young secondary forests, and consequently can support higher diversity (Brockerhoff *et al.*, 2008). In this study, forest had the longest “time since disturbance”, having been protected from logging since 1888. Forest supported the most distinctive invertebrate assemblage (based on ANOSIM results), with fynbos and pine plantation probably having roughly equivalent disturbance histories, based on time since last fire (in fynbos) and time since last planting (in pine). Actual dates of last fire and planting were not available for all sites

sampled, and so disturbance history was not included as an explanatory variable in the above analyses, although the relationship is intuitively evident.

The invertebrate communities of pine plantations were more similar to those of forest than fynbos. Pine plantations, by offering a comparable litter and dead wood microhabitat to that of forest, extend the distribution range of numerous forest invertebrates, including rare and endemic species. In New Zealand, for example, plantations provide habitat for rare species, such as kiwi, bats and falcon (Maunder *et al.*, 2005). Plantations may also buffer edge effects for small forest patches and increase connectivity (Brockhoff *et al.*, 2008). This may be particularly relevant for forest patches on the Cape Peninsula, which are embedded in a city landscape mosaic (Pryke & Samways, 2009b). A future study looking at the conservation implications of plantation edge impacts on native forest and fynbos invertebrate communities, in which the magnitude and penetration of edge effects are quantified (Ewers & Didham, 2006), is recommended. Although increased available habitat and connectivity between patches is often desirable in biodiversity conservation, connectivity may have negative consequences. Afrotemperate forest patches across the Cape Peninsula are naturally small and fragmented (Mucina & Geldenhuys, 2006) and so the connectivity provided by these alien plantations has several possible disadvantages. Plantations may facilitate the spread of weeds, pathogens, pests and inappropriate genetic material (MacDonald, 2003). Providing connectivity between diverging metapopulations of habitat-restricted taxa may facilitate genetic mixing between populations and thus reduce the evolutionary potential of such populations, which is not desirable for biodiversity conservation. For many forest species, the fynbos matrix surrounding forest islands may be an effective barrier to migration and gene flow. Under natural conditions, these Afrotemperate forest patches also characteristically have sharp edges, maintained by frequent fires in the fynbos matrix. The establishment of pine plantations has altered the natural fire regime in fynbos (van Wilgen, 2009), with knock-on effects for invertebrate communities.

The impact of pine plantations may also be negative for many fynbos invertebrates, which cannot colonise and persist in the dense litter and closed canopy tree environment of plantations. Plantation edge effects in a range of biotic variables may negatively affect ecological processes in fynbos, as they do in other landscapes (Pawson *et al.*, 2008). Changes in invertebrate composition are often strongly correlated with a gradient from open (*e.g.* fynbos) to closed (*e.g.* pine plantation) canopy conditions (Samways *et al.*, 1996; Pawson *et al.*, 2010). Of particular concern is the impact of pine on Peninsula Granite Fynbos and its associated invertebrate community, because this vegetation type is listed as 'Endangered', with very little remaining (Granite Fynbos covers only 2% of the Fynbos Biome), and the remaining

untransformed Peninsula Granite Fynbos is senescent and invaded by Afrotemperate forest trees (Rebelo *et al.*, 2006). Once again, attention must be drawn to the fact that the two Peninsula Granite Fynbos sites sampled (Sites 6 and 8 in Kirstenbosch) represent the last remaining accessible untransformed patches of Peninsula Granite Fynbos on Table Mountain. All pine plantation sites sampled were originally planted over Granite Fynbos, which generally occurs at lower altitudes and on richer soil than Sandstone Fynbos. However, pine plantation sites clustered closer to Sandstone Fynbos sites than to Granite Fynbos sites in the MDS ordination. The Granite Fynbos invertebrate community (at Sites 6 and 8) was very different from communities in other vegetation types. This suggests that the fynbos invertebrate species that have established in these pine plantations come from the surrounding, often contiguous, Sandstone Fynbos patches. The true Peninsula Granite Fynbos litter invertebrate community may already be lost on the Cape Peninsula. However, small sample size for Granite Fynbos limits the generalisation of this finding.

Vegetation type (or structure) was the most intuitively parsimonious environmental variable explaining invertebrate community composition among habitats, even though other environmental variables were not tested statistically. Vegetation structure (forest and fynbos) and elevation have also previously been identified as the most important variables for both surface-active invertebrates (Pryke & Samways, 2010) and aerial and foliage invertebrates (Pryke & Samways, 2008) on Table Mountain. Fynbos type (namely Granite Fynbos and Sandstone Fynbos) appears to strongly influence the invertebrate community, with fynbos sites separating into three clusters: Peninsula Granite Fynbos, Peninsula Sandstone Fynbos and recovering Peninsula Sandstone Fynbos. However, this is confounded to some degree not only by the low number of site replicate, but also by the significant positive spatial autocorrelation at the shortest distance class in fynbos, since the only two Peninsula Granite Fynbos sites sampled are in close proximity to each other, separated by the forest patch in Nursery Ravine at Kirstenbosch. Despite the obvious statistical limitations of such low sample size ( $n = 2$  Granite Fynbos sites), which are confounded by positive spatial autocorrelation (Legendre & Legendre, 1998), this should not distract from the management implications of conserving the irreplaceable invertebrate community in this Endangered vegetation (Rebelo *et al.*, 2006).

Sites 6 and 8 at Kirstenbosch were the only Granite Fynbos sites sampled, because there are no other suitable, accessible, untransformed Peninsula Granite Fynbos sites left. All other low altitude areas that could support Peninsula Granite Fynbos (based on their geology) have been transformed into plantations or vineyards. Thus any further sampling in Granite Fynbos could only take place at Kirstenbosch and would then constitute pseudoreplication.

These two sites were also the only fynbos sites not in close proximity to pine plantations, as there are no plantations in, or above, Kirstenbosch National Botanical Garden. By comparison, other areas sampled had pine plantation on the lower slopes, buffering the National Park from the suburbs and/or vineyards. A possible further explanation for differences in community composition between the two Granite Fynbos sites above Kirstenbosch Botanical Garden, compared to other sites, could be the influence of the botanical garden itself. Pryke & Samways (2009b) report very high species richness and abundance of both ground-dwelling and aerial invertebrates in Kirstenbosch National Botanical Garden. They attribute this difference to the fact that the botanical garden is cultivating many indigenous plants, which provide habitat for a wide range of invertebrate species, and comprises a pesticide-free, well-watered and well-managed source of invertebrates to colonise adjacent areas of Table Mountain. To confound matters further, Sites 6 and 8 were moribund and invaded by some Afrotropical forest trees as a result of the long-standing fire exclusion policy in place in Kirstenbosch. Under more natural conditions fynbos maintains dominance in the landscape through regular natural burning, since fire excludes forest tree species (Rebelo *et al.*, 2006 and references therein). Nevertheless, these sites showed very little community similarity with either forest or pine plantation.

Sandstone Fynbos communities also formed a separate cluster, as did recovering Sandstone Fynbos communities previously under pine. Interestingly, the latter clustered closer to pine plantation communities than to other fynbos sites, suggesting that they share more taxa in common with pine plantation than with other fynbos sites. This was confirmed by omitting Sites 3 and 30 in ANOSIM, which resulted in a much higher *R*-value separating fynbos and pine plantation than when these sites were included in the analysis. The impacts of pine plantations appear to persist long after clear-felling, as seen from the community composition of Sandstone Fynbos sites previously under pine. Afforestation of natural non-forest land, such as fynbos, is generally viewed as detrimental to conservation (Brockerhoff *et al.*, 2008). These interpretations must however be weighed against the low number of site replicates for these habitats.

Pine plantation had more species in common with forest than with fynbos, as was expected, since the litter and dead wood microhabitats, soil moisture levels and shading effects in pine plantation more closely resemble those in forest than those in fynbos habitats. Pine plantations may therefore approximate a forest habitat for ground-dwelling invertebrates. However, while apparently mimicking forest, pine plantations in fact supported virtually no Cape Peninsula endemic species, with habitat generalists and ecologically-tolerant species possibly dominating the community. Plantations often support fewer forest specialist species (*e.g.*

carabid beetles) than forest generalist species, which occur across various habitats (Magura *et al.*, 2000). Therefore, pine plantations are actually a low quality habitat for leaf litter invertebrate fauna, in terms of assemblage composition.

The high number of unique species found in forest and fynbos (when compared to pine plantation) may reflect the presence of many true habitat specialists. Conversely, pine plantation relies on donor habitats (including urban and agricultural habitats) as a source of immigrants. However, most of these unique species in native habitats were represented by singletons or doubletons, and probably include tourists, incidental catches, or genuinely rare species. It may also reflect the lack of sampling saturation, despite the fairly extensive sampling effort. Nevertheless, the sampling methods employed targeted the litter fauna, which generally has low vagility and would be less impacted by visitors (typically flying insects).

Species turnover was high both within and between habitats and was, as predicted, somewhat lower between sites in pine plantation than among sites in either forest or fynbos. Individual species generally show naturally patchy distributions (Hammond, 1994; Gotelli & Colwell, 2001). This patchiness (*i.e.* heterogeneity) can be found at all spatial scales (Legendre & Legendre, 1998). High turnover is to be expected for ants (Botes *et al.*, 2006a) and other ground-dwelling invertebrates (Ferrier *et al.*, 1999; Uys *et al.*, 2009). Yet, even more mobile invertebrates, such as Monkey beetles (Scarabaeidae: Hopliini) show high species turnover (beta diversity) in southern Africa (Picker & Midgley, 1996; Colville *et al.*, 2002; Colville, 2009). The winter rainfall biomes of southern Africa, especially fynbos, show exceptional beta diversity in floral diversity patterns (Cowling *et al.*, 1989; Cowling, 1990; Simmons & Cowling, 1996; Cowling *et al.*, 1998; Cowling *et al.*, 1999). This high floral species turnover is likely to be mirrored in many invertebrate taxa, albeit less so in ground-dwelling and litter taxa, than in pollinators and other foliage- and aerial-dwelling taxa. Positive relationships between fynbos plant species richness and insect species richness have been reported for a few, non-ground-dwelling taxa (Wright & Samways, 1998; Procheş & Cowling, 2006). However, Cape Peninsula endemic invertebrates show only a weak significant relationship ( $R^2 < 3\%$ ) with plant richness, since the majority of these endemic invertebrates are neither highly mobile nor concentrated in fynbos (Picker & Samways, 1996). This implies that both Afrotropical forest and fynbos must be carefully managed and conserved on the Cape Peninsula, in order to protect this globally significant plant and invertebrate diversity.

Based on a survey of arthropods in Gabon, Basset *et al.* (2008) recommended reporting both species richness and turnover, and cautioned against focussing on species richness alone to avoid drawing misleading conclusions about arthropod assemblages in conservation studies.

In general, beta diversity should be higher for taxa that are poor dispersers, because dispersal ability is inversely related to the rate of species turnover (Qian, 2009; Jimenez-Valverde *et al.*, 2010). Arthropods exhibit greater spatial turnover than vertebrates (Ferrier *et al.*, 1999). Similarly, within the global distribution of vertebrates, beta diversity of birds and mammals is less than that of amphibians and reptiles (McKnight *et al.*, 2007; Qian, 2009).

In addition to dispersal ability of organisms, landscape features also influence beta diversity patterns. The highest beta diversity for birds in South Africa coincides with transition zones between biomes (van Rensburg *et al.*, 2004). The highest beta diversity for New World birds and mammals has been recorded in mountainous areas, with altitude the best predictor of beta diversity (Melo *et al.*, 2009). Thus geographical distance alone is not always enough to explain species turnover in terrestrial ecosystems and other spatial and environmental processes, especially topography, should be considered (Jimenez-Valverde *et al.*, 2010).

Species turnover both within and between habitats did not increase with distance between sites. The cluster analysis and MDS ordination suggest that invertebrate species distributions are not clustered along the north-south spatial gradient across the Cape Peninsula, the long-axis of which runs north-south, in any of the habitats sampled. Distance alone also did not explain species turnover (measured as  $\beta_{sim}$ ) for ground-dwelling flightless invertebrates in Afrotemperate forest patches in the Drakensberg Mountains, South Africa (Uys *et al.*, 2009). These authors reported significant positive spatial autocorrelation between forest patches at distances of less than 1.3 km apart, reflecting the similarity of assemblage composition of sites within valleys. Spatial autocorrelation at small scales (short distances) is reportedly common for soil-dwelling invertebrates in natural (forest and wetland) and managed (pasture and cropland) environments (Minor, 2011 and references therein). Dispersal limitations may only prove relevant at larger (regional) spatial scales, so that the 12 km north-south distance between the furthest sites sampled in this study may not be a meaningful dispersal limitation.

While there is little evidence for distance-dependent community composition of ecosystems over relatively small spatial scales, both environmental variation and geographical distance between sites at larger spatial scales determine patterns of species turnover for ground-dwelling ants, beetles and spiders in north-east New South Wales, Australia (Ferrier *et al.*, 1999) and for macroinvertebrate pond communities in Oxfordshire, UK (Briers & Biggs, 2005). Hughes *et al.* (2000) offer two extremes as explanations for changes in species composition across a landscape: either gradual changes along spatially autocorrelated gradients of environmental variables, or sudden changes between discrete habitat types. More often (and most probably in this case), turnover is likely to reflect a combination of these two



extremes. Afrotropical forest on the Cape Peninsula is naturally fragmented, being restricted to fire-protected rocky ravines (Rebello *et al.*, 2006). Given the low vagility of the largely wingless, moisture-dependent litter fauna, species turnover would be predicted to be high, possibly higher than in more open and contiguous fynbos habitat. This was not supported by the turnover values for forest sites, which were on average slightly lower than those for fynbos sites. This may reflect the disturbance history and vegetation compositional differences in fynbos. Many of the Cape Peninsula endemic taxa, a fair number of which are litter fauna, are widely distributed across the Peninsula (Picker & Samways, 1996). Alpha and beta diversity when considered in concert suggest that the true invertebrate richness is lower in pine plantations than in native vegetation on the Cape Peninsula.

#### *Cape Peninsula endemic invertebrates*

The nine Cape Peninsula endemic invertebrates recorded here are likely an underestimate of true invertebrate endemism at the study sites, since most taxa were only identified to morphospecies. Even within taxa identified by taxonomists, many morphospecies could not be assigned names, for a number of reasons. For example, the cockroach fauna of South Africa is incompletely known, only part of the fauna has been described, and these descriptions are often insufficient for a clear species determination (H. Bohn pers. comm., 2010). One new cockroach genus and a new species of *Ectobius* (Blattellidae) were collected in this study, and may well represent new Cape Peninsula endemics. Similar taxonomic limitations restricted the identification of springtails. Less than half of the springtail species collected in this study could be assigned names by a collembolan taxonomist and many of these may turn out to be undescribed Cape Peninsula endemics. Most publications on collembolan taxonomy in the region come from sporadic and scant collecting, often as by-catch from studies on other focal taxa (E. Bernard pers. comm., 2010).

The number of endemic species recorded is also likely to be underestimated, because endemic invertebrates may be rare and/or localized. The 111 invertebrate species recorded in the literature as being endemic to the Cape Peninsula (Picker & Samways, 1996) is also certainly an underestimate, because little or no information exists for several invertebrate taxa. The true number of Cape Peninsula endemic invertebrates may also be underestimated because taxa previously considered to have widespread distributions may in reality comprise species complexes. Several recent molecular analyses on what were previously considered to be widespread species have revealed extensive cryptic species. For example, the velvet worm *Peripatopsis balfouri*, which occurs on the Cape Peninsula and elsewhere, has recently been

found to have six evolutionary distinct lineages (Daniels *et al.*, 2009), one of which was present in three forest sites and one pine plantation site in this study. Cryptic species are also likely to occur in other taxa with limited dispersal capability and desiccation sensitivity (such as molluscs and earthworms), that are forest specialists and that occur ecotypically with Onychophora (Daniels *et al.*, 2009).

Of the 111 Cape Peninsula endemic species reported by Picker & Samways (1996), only a fraction would be found in the habitats sampled, since many are aquatic, cave-dwelling, or not ground-dwelling. Some of the species recorded in the literature (Picker & Samways, 1996) may also be extinct, since many of the original records date back many decades. For example, the velvet worm, *Peripatopsis leonina*, has not been collected from its former habitat on Signal Hill since it was described in 1900, despite numerous search attempts, and is now considered extinct (Hamer *et al.*, 1997; Daniels *et al.*, 2009). Other species sharing this litter habitat might have suffered the same fate.

Two Cape Peninsula endemic cockroach species were found to be widespread and abundant in fynbos, but were not recorded in pine plantation. Afforestation may have had a negative impact on these cockroaches, by reducing suitable available habitat. Neither cockroach was collected at Site 3, a small patch of recovering Sandstone Fynbos that was previously under pine. The scorpion *Uroplectes insignis* was the only Cape Peninsula endemic species collected in all three habitats. Although widespread in forest and fynbos, it was only collected in pine plantations in Newlands Forest. This implies that alien plantations may not offer suitable surrogate habitat for most Cape Peninsula endemic invertebrates, in spite of forest and pine plantation sharing a fairly high number of species. Until recently, *U. insignis* was known only from forest on Table Mountain (Prendini, 2005). Raharinjanahary (2007) collected *U. insignis* in both Afrotropical forest and pine plantation in Newlands Forest, at the same sites sampled in this study. Pryke & Samways (2010) also report *U. insignis* as widespread in fynbos and forest across Table Mountain. This species may be expanding its range, possibly in the absence of frequent fires on the eastern slopes of the mountain, but more plausibly has simply been inadequately surveyed in the past.

#### *Alien invertebrates*

The 19 alien species identified is also likely to be an underestimate of the true alien fauna on the Cape Peninsula, since most taxa in this study were identified only to morphospecies, and several species are not yet named, so their origin and distribution are unknown (cryptogenic). No previous study has focused on alien invertebrates on the Cape Peninsula, although the

Argentine ant (*Linepithema humile*) has received some attention (Picker & Samways, 1996; Ratsirarson *et al.*, 2002; Raharinjanahary, 2007; Pryke & Samways, 2010), and 15 other alien invertebrate species were collected in Newlands Forest by Raharinjanahary (2007). Table Mountain is among the most thoroughly sampled areas for invertebrates in southern Africa (Picker & Samways, 1996; Hamer & Slotow, 2002), yet knowledge of its invertebrate fauna remains poor. For example, the world's only known jumping cockroach was recently discovered on Table Mountain (Bohn *et al.*, 2010). The value of, and necessity for, a detailed inventory of alien invertebrates in a national park of World Heritage status and global biodiversity significance seems obvious, and requires urgent attention. Impacts of this alien fauna on the endemic Cape Peninsula invertebrates are a major conservation concern.

European wasps (*Vespula germanica*), a well-known invasive, have received some attention in the Western Cape Province (Tribe & Richardson, 1994), but their distribution and status on the Cape Peninsula requires reassessment. Pryke & Samways (2009b) collected only two individuals of European wasps in an 18 month sampling period (July 2005 – January 2007); both in natural vegetation, suggesting that this species may not inhabit pine plantations and that populations may have declined on the Cape Peninsula. However, 32 individuals of European wasps were collected during the five month sampling period (September 2008 – February 2009) in this study, despite the fact that the sampling methods used did not target flying insects. Although numbers collected were lower in pine plantation, European wasps were present in forest (three sites), fynbos (two sites) and pine plantation (two sites), and in five of the eight areas sampled. A small nest was also observed in a decaying pine log in pine plantation (Site 22) in Orange Kloof (C. Uys pers. obs., January 2009), suggesting that European wasps can survive in pine plantation.

Since flying insects were not targeted by the collecting methods used in this study, the abundance of European wasps is most likely underestimated and biased, and these findings must be interpreted with due caution. It does, however, highlight the need for an in-depth, targeted study on this species. Most individuals in this study were caught in sugar-baited ant traps which would certainly underestimate their presence and abundance as they are not strictly ground-dwelling species, although they do hunt for invertebrate prey on the litter surface, and are attracted to a carbohydrate source (Harris & Oliver, 1993; Sackmann *et al.*, 2000; Kasper *et al.*, 2004). European wasps also occur in the Stellenbosch area and in Jonkershoek Nature Reserve (C. Uys pers. obs., March 2010), some 50 km inland, suggesting that they may be widespread and well-established in a range of vegetation types in the Western Cape Province.

Argentine ants invade new areas by dispersing along roads and water-courses (Human *et al.*, 1998). In fynbos, their spread and successful establishment are closely linked with the road accessibility of an area, such that most of the old records of Argentine ants in fynbos come from residential areas, picnic sites and refuse dumps (De Kock & Giliomee, 1989). Table Mountain National Park has many mountain streams and is serviced by a network of roads and well-used paths, especially in the pine plantations, all potentially facilitating the spread of this invasive alien species into native vegetation. It appears as if Argentine ants can establish and maintain colonies in fynbos, since in this study at least one confirmed nest was found in fynbos, and the species was present in seven of the eight fynbos sites sampled. Pryke & Samways (2010) also recorded Argentine ants in fynbos at similar elevations (240-400 m a.s.l.) on the western, southern and eastern slopes of Table Mountain. Raharinjanahary (2007) reports Argentine ants only below 350 m in Newlands Forest. Both of these studies are within the altitudinal range at which Argentine ants were collected in this study, *i.e.* 130-520 m a.s.l. (although they were most abundant below 400 m a.s.l.). It is of concern that the abundance and number of nests was much higher in forest than in pine plantation, where Argentine ants were expected to be most abundant. Argentine ants have probably been well established in Afrotropical forest on the Cape Peninsula for many years, and have been recognized as a threat to native invertebrate diversity in previous studies (Picker & Samways, 1996; Ratsirarson *et al.*, 2002; Raharinjanahary, 2007; Pryke & Samways, 2010).

### *Conclusion*

Studies assessing both species richness and community composition often show more negative impacts of plantations on community composition than studies focussed on species richness alone, even though the literature is biased towards assessing species richness, rather than community composition (Su *et al.*, 2004). Inferences on the impacts of plantations based on species richness assessments alone should be interpreted with caution, especially in assessments of arthropod diversity (Basset *et al.*, 2008). Nevertheless, this study adds to the growing body of evidence showing that exotic plantations have lower species richness and different community assemblages, compared to neighbouring native forest, in South Africa and globally.

More importantly, pine plantations on the Cape Peninsula may also have negative impacts on the fynbos-specialist invertebrate community, whose available habitat has diminished through afforestation. Pine plantations have both direct effects on fynbos invertebrate communities through habitat-replacement, and indirect effects through negative on-

site and off-site effects. Exotic plantations are considered detrimental when afforestation takes place in natural non-forest land (Brockerhoff *et al.*, 2008), even though they may hold biodiversity value in some circumstances (*e.g.* Brockerhoff *et al.*, 2008), and may provide a novel habitat for native forest species (Quine & Humphrey, 2010).

Although the pine plantations sampled in this study are not 'biological desserts' (Bonham *et al.*, 2002; Hartley, 2002; Lachat *et al.*, 2006; Brockerhoff *et al.*, 2008), and do not create a binary landscape of suitable versus unsuitable habitat (Ricketts, 2001), they hold low conservation value in this landscape. Compared to forest and fynbos, pine plantations supported much lower invertebrate abundance, fewer unique species, only one Cape Peninsula endemic species, about the same number of alien invertebrate species, and lower species turnover (beta diversity). The current pine plantation litter community has more in common with Afrotropical forest, and less with the original Granite Fynbos community which was displaced by the pine plantation.

## CHAPTER 4. IMPACTS OF ARGENTINE ANTS AND OTHER ALIEN INVERTEBRATES ON NATIVE GROUND-DWELLING INVERTEBRATES ON THE CAPE PENINSULA

### Introduction

The British ecologist, Charles Elton, prophetically warned of the dangers arising from invasive alien species: “The real thing is that we are living in a period of the world’s history when the mingling of thousands of kinds of organisms from different parts of the world is setting up terrific dislocations in nature. We are seeing huge changes in the natural population balance of the world” (Elton, 1958). Invasive alien species are now widely recognised as the second greatest threat to global biodiversity, after habitat destruction (Wilcove *et al.*, 1998; Simberloff, 2001). Despite this, the degree, impacts and consequences of invasion by most invasive alien species, particularly invertebrates, remain poorly understood. In a review of the ecological effects of invasive alien insects, Kenis *et al.* (2009) report that only 72 invasive insect species had been studied worldwide, of which 54 showed evidence for ecological impacts in the field. Although the number of invasive insect species known to have an effect on biodiversity appears to be disproportionately low, this most likely reflects a lack of investigations, rather than a lack of effect, since the vast majority (over 80%) of studies conducted on invasive insects do report significant effects (Kenis *et al.*, 2009). This introduction reviews the invasion history and impacts of invasive ants and other alien invertebrates, focusing on the litter taxa collected in this study.

The ecological impacts of invasive alien species affect all levels of organization (genetic, population, community and ecosystem levels) and differ among herbivores, predators, parasites, parasitoids and pollinators (Kenis *et al.*, 2009). Through collective direct and indirect effects, invasive alien species can displace native species, disassemble the remaining communities (Sanders *et al.*, 2003) and disrupt various ecosystem processes (O’Dowd *et al.*, 2003). In a review of case studies of biological invasion from 1980 to 2006, spanning 892 species in most taxonomic groups from around the world, 36.3% of studies focussed on the biology and ecology of invertebrates, with the Argentine ant (*Linepithema humile*) receiving the most research attention among terrestrial invertebrates (Pyšek *et al.*, 2008). Another review of 403 primary research papers dealing with the impacts of invasive insects (1900-2007 inclusive) revealed that 41% concerned invasive ants, with two species (Red imported fire ant, *Solenopsis invicta*, and Argentine ant, *L. humile*) dominating the literature (Kenis *et al.*, 2009). These two species, together with the Yellow crazy ant (*Anoplolepis gracilipes*), Big-headed ant (*Pheidole megacephala*) and Little fire ant (*Wasmannia auropunctata*) are listed among the 100 of the

*world's worst invasive species* (Lowe *et al.*, 2000). More recently, other invasive ant species have received more attention (reviewed in Lach & Hooper-Bùi, 2010). Invasive ants are a globally-pervasive ecological problem because of their expanding geographic ranges, high propagule pressure, high local abundances and ability to disrupt ecosystem processes (Holway *et al.*, 2002).

The most widely documented impact of ant invasions is the displacement of native ants, although only a handful of studies use direct experimental approaches to document such displacements (Holway *et al.*, 2002). Most reports of decreases in native ant species richness with invasion come from studies of Red imported fire ants and Argentine ants (Holway *et al.*, 2002). Argentine ants have reduced native ant diversity in California (*e.g.* Holway, 1998), Hawaii (Cole *et al.*, 1992), Australia (Rowles & O'Dowd, 2007), Japan (Touyama *et al.*, 2003) and other invaded locations. Argentine ants have also been reported to reduce ant species richness in South African fynbos and to replace dominant native ants, in particular, ground-foraging, seed-dispersing ant guilds (Bond & Slingsby, 1984; Parker-Allie *et al.*, 2008).

The presence of Argentine ants in fynbos is therefore of urgent conservation concern, because up to 30% of the fynbos flora (including 50% of the Proteaceae) depends on seed dispersal by ants (Bond & Slingsby, 1984). Argentine ants include seed in their diet, but do not bury them, unlike many of the native ants (Christian, 2001). This is problematic, because the two abundant native ant species (*Anoplolepis custodiens* and *Pheidole capensis*) that are the most effective dispersers of large-seeded proteas are displaced or eliminated by Argentine ants (De Kock & Giliomee, 1989; Christian, 2001; Witt *et al.*, 2004). This results in substantially lower post-fire recruitment of large-seeded fynbos species. Ant species such as *Meranoplus peringueyi* and *Tetramorium quadrispinosum* that are able to coexist with Argentine ants (Luruli, 2007) are not big enough to carry large, heavy seeds (Christian, 2001). This leads to altered plant species composition in invaded fynbos communities, due to the localised decline of large-seeded myrmecochorous plant species. Similar reduced seed dispersal has been reported in California in areas invaded by Argentine ants, compared to control areas dominated by native harvester ants (*Pogonomyrmex subnitidus*) that also disperse seeds (Carney *et al.*, 2003).

Exploitative and interference competition are two of the most important mechanisms contributing to the competitive nature of Argentine ants, and explain their ability to displace native ant species (Human & Gordon, 1997). Argentine ants show rapid recruitment, high abundance, high territoriality and intense interspecific aggression (Rowles & O'Dowd, 2007). Native ant species with similar niche preferences to Argentine ants are most vulnerable to

displacement. Epigaeic (above-ground foraging) species are consequently more affected than hypogaeic (below-ground foraging) species (Harris, 2002).

Argentine ants, when numerically dominant, also surpass native ant species in exploiting resources, because they show generalist feeding behaviour and are omnivorous, consuming a variety of food resources. Argentine ants display flexible patterns of resource use and a shift in diet after establishment, as a result of resource depletion (Tillberg *et al.*, 2007). Although they are amongst the most carnivorous of ants (Tillberg *et al.*, 2007), they also feed extensively on liquids (Zee & Holway, 2006), showing a preference for hemipteran honeydew (Silverman & Brightwell, 2008). The monopolisation of carbohydrate-rich resources, such as plant and hemipteran exudates, has been reported for all of the most important invasive ant species (Lach, 2003). This is thought to contribute to their invasion success (Holway *et al.*, 2002; O'Dowd *et al.*, 2003; Rowles & Silverman, 2009; Lach *et al.*, 2010). Argentine ants generally choose nest sites in close proximity to a food source, but are able to forage up to 60 m away from their nest (Silverman & Brightwell, 2008).

Argentine ants are unicolonial, forming supercolonies with thousands of workers and multiple queens, distributed among interconnected nests (Tsutsui & Suarez, 2003; Holway & Suarez, 2004; Walters & Mackay, 2005; Heller *et al.*, 2006). In contrast, native ants typically live in small colonies with a single nest, with only one queen per nest, and colonies react antagonistically to non-colony members (Hölldobler & Wilson, 1990). Local-scale colony spread of Argentine ants occurs via budding, rather than by queens using long-distance dispersal through nuptial flights (Silverman & Brightwell, 2008). This ensures that dispersing queens are accompanied by high numbers of workers, which then dominate and suppress native ant species along the colony's expanding border. Accordingly, interference competition, resource exploitation, and highly polygynous (multiple queens per nest) and polydomous (multiple nests per colony) life history traits all contribute to the invasion success of Argentine ants.

Behavioural and life history traits, niche dimensions and biogeographic affinities are the basis on which functional groups have been assigned for ant genera. Niche dimensions, such as diet, nest location and time of foraging are indicative of broad-scale, worldwide responses of the component taxa to disturbance and environmental stress (Andersen, 1997a). Argentine ants have been assigned to the Dominant Dolichoderinae functional group, members of which are characteristically abundant, highly active and aggressive ants, with a strong competitive influence on other ant species (Andersen, 1997a). Not all dolichoderines show behavioural dominance, and the Dominant Dolichoderinae functional group is not represented in the native southern African ant fauna, where behavioural dominance has instead evolved in the formicines



(*Anoplolepis custodiens* group) and some myrmecines (*Pheidole*, *Monomorium* and *Crematogaster* spp.) (Majer *et al.*, 2004; Parr, 2008). Dominant Dolichoderinae are also absent in cool-temperate regions elsewhere (except for parts of Australia) and formicines (*e.g.* *Formica*) dominate throughout the Holarctic. Subordinate Camponotini (*e.g.* *Camponotus*) co-occur with Dominant Dolichoderinae, because they are behaviourally submissive, have a large body size and often forage nocturnally (Andersen, 1997a). *Camponotus* spp. are also naturally subordinate in the presence of behaviourally dominant southern African ants (Parr, 2008). Opportunists (*e.g.* *Tetramorium*) can also coexist with Argentine ants, because they generally occur in disturbed habitats that support low ant diversity (Hoffmann & Andersen, 2003). Conversely, Tropical Climate Specialists (*e.g.* *Tetraponera*) and Hot or Cold Climate Specialists (*e.g.* *Meranoplus* and certain *Monomorium* spp.) favour habitats where Dominant Dolichoderinae are not abundant (Andersen, 1997a). Generalized Myrmecinae show a range of responses to Argentine ants and other Dominant Dolichoderinae, from co-occurrence through little or no direct interaction (*e.g.* *Crematogaster*: Addison & Samways, 2000; Brown, 2000), co-occurrence through the use of chemical secretions that repel Argentine ants (*e.g.* *Monomorium*: Holway, 1999; Hoffmann & Andersen, 2003), to displacement by Argentine ants due to similar resource requirements (*e.g.* *Pheidole*: Bond & Slingsby, 1984; Witt & Giliomee, 1999).

These impacts are of conservation concern, because Argentine ants are well-established in natural environments on the north-eastern Iberian Peninsula (Roura-Pascual *et al.*, 2010), in coastal California (Holway & Suarez, 2006) and in North Carolina (Rowles & Silverman, 2010). They are equally well-established in protected areas in the Western Cape (Luruli, 2007), including Jonkershoek Nature Reserve near Stellenbosch (Witt, 1993), Kogelberg Biosphere Reserve near Hermanus (Bond & Slingsby, 1984; Christian, 2001), Helderberg Nature Reserve outside Somerset West (Boonzaaier, 2006) and Table Mountain National Park in Cape Town (Picker & Samways, 1996; Pryke & Samways, 2009b; 2010). The extent of impacts caused by Argentine ant invasion in the Western Cape is not yet fully described or understood.

The impacts of invasive ants are not always simply detrimental. Some studies show no, or only weak, community-level effects (Holway, 1998; Walters, 2006; Rowles & Silverman, 2010). Ground-dwelling taxa that prey on ants may benefit trophically from ant invasions; for example, ant-lions in California (Glenn & Holway, 2008) and myrmecophagic spiders in Japan (Touyama *et al.*, 2008). The magnitude of the impacts of Argentine ants on native, non-ant invertebrates, especially ground-dwelling arthropods, is often proportional to the degree of evolutionary coexistence of the native invertebrate community with aggressive native ant

species (Hoffmann & Parr, 2008 and references therein). Island faunas that lack native ants suffer the most devastating effects from invasive ants. In Hawaii, spiders and predatory beetles (especially native carabids) are especially negatively affected by invasive ants (Cole *et al.*, 1992; Holway *et al.*, 2002; Liebherr & Krushelnycky, 2007), and compositional changes occur most often among endemic arthropods (Krushelnycky & Gillespie, 2008). Impacts may also be greater on the edge of habitat fragments. For example, the abundance and species richness of Acari, Hemiptera, Coleoptera, Diptera and non-ant Hymenoptera are negatively correlated with Argentine ant abundance in urban habitat fragments in coastal southern California (Bolger *et al.*, 2000).

Soft-bodied taxa, such as Collembola and larval Lepidoptera, appear to be exceptionally vulnerable to invasive ants (Cole *et al.*, 1992; Human & Gordon, 1997; Rowles & O'Dowd, 2009). Woodlice and cockroaches are able to persist in the presence of invasive ants, probably because they are protected by their hard, often armoured exoskeletons (Hoffmann & Parr, 2008), and may even show greater abundance at invaded sites (Human & Gordon, 1997; Bolger *et al.*, 2000; Walters & Mackay, 2003). Amphipods are either more abundant in invaded areas (Walters & Mackay, 2003), or show no change in numbers with invasion (Walters, 2006) in South Australia. Psocoptera and other scavengers may increase in abundance with invasion, because the versatility of their diets helps reduce direct resource competition with invasive ants, and an increased ant biomass means that more dead ants and prey remains are available for scavengers to feed on (Bolger *et al.*, 2000; Walters & Mackay, 2003; Rowles & O'Dowd, 2009). Many honeydew-producing Homoptera, such as scale insects, mealybugs, aphids and membracids, readily establish symbiotic relationships with alien ants (Holway *et al.*, 2002).

This ability to establish mutualisms with native membracids enables Argentine ants to interfere with natural pollination mechanisms. In fynbos, Argentine ants are attracted to native honeydew-producing membracids (*Beaufortiana* sp.) in *Protea* inflorescences, and this mutualism facilitates pollinator deterrence by Argentine ants (Lach, 2007). *Protea nitida*, and probably many other fynbos *Protea* species, suffer a decline in insect pollinator visitation and a resultant decline in seed set in the presence of Argentine ants (Lach, 2007). Argentine ants also consume floral nectar, which further negatively affects arthropod pollinators (Visser *et al.*, 1996). Pollen-limited, arthropod-pollinated plants are the most susceptible to invasive ants; as evidenced in other parts of the world. In Hawaii, Argentine ants threaten insect-pollinated plants, such as *Metrosideros polymorpha*, by depleting floral nectar and displacing native bee pollinators (Cole *et al.*, 1992; Lach, 2005; 2008). In Spain, Argentine ants threaten *Euphorbia characias* by decreasing visitation times by fly pollinators and overall numbers of arthropod

visitors (Blancafort & Gomez, 2005) and by displacing native ant pollinators (Blancafort & Gomez, 2006).

By displacing native ants, Argentine ants also have the potential to disrupt the obligatory associations between larvae of myrmecophilous lycaenid butterflies and their native ant hosts (Heath & Claassens, 2003). Myrmecophiles spend at least part of their life cycle in ant colonies, as commensals, mutualists, or parasites (Hölldobler & Wilson, 1990). On Table Mountain (Cape Peninsula, South Africa), at least 12 of the 27 Lycaenidae are myrmecophiles, several of which are regional endemics (*e.g. Thestor*) and on the IUCN Red List of Threatened Species. Hence, potential disruptions to these ant-butterfly mutualisms by invasive ants could further threaten these already sensitive species. In Australia, 39 of the 56 obligate lycaenid myrmecophiles have distributions that overlap with Argentine ants, or other invasive ants, and it is not yet known whether these invasive ants tend, or prey on, the lycaenid larvae (Lach & Thomas, 2008). Argentine ants more likely indirectly affect lycaenid larvae by suppressing numbers of native host ant species.

Argentine ants even displace vertebrates (Kenis *et al.*, 2009). Anecdotal, correlative and, more recently, experimental evidence show adverse effects of various invasive ants on birds, mammals and herpetofauna (summarised in Lach & Hooper-Bùi, 2010). The impacts of Argentine ants on vertebrates in southern Africa have not yet been investigated and, although beyond the scope of this study, may be important in cases of rodent pollinated flowers (Wiens & Rourke, 1978). Several proteas have ground-hugging flowers that are adapted for pollination by ground-dwelling rodents that also feed on nectar and insects visiting the inflorescences. Many other proteas are brightly coloured and carry their blooms high in the tree to attract avian pollinators, such as Cape Sugarbirds. High numbers of Argentine ants may reduce the visitation rates of these pollinators.

The European wasp (also known as German wasp or Yellowjacket), *Vespula germanica*, is native to Eurasia and North Africa (Archer, 1998). It has successfully invaded and established populations in the United States, Canada, Ascension Island, New Zealand, Australia, Tasmania, Chile, Argentina and South Africa (Archer, 1998). *V. germanica* was unintentionally introduced to the Western Cape Province, South Africa, probably prior to 1970, and was first recorded on the Cape Peninsula in 1974 (Whitehead & Prins, 1975). It has established populations in relatively undisturbed natural vegetation on the Cape Peninsula (Richardson *et al.*, 1992), although these are mostly in moist localities associated with mountains, such as in dense forest on Table Mountain (Whitehead & Prins, 1975). Fynbos is considered a marginal habitat for the establishment of colonies, as a result of low arthropod prey abundance (Tribe & Richardson,

1994). Compared to New Zealand and Tasmania (Davidson, 1987), expansion in South Africa has been very slow, despite the entire eastern coastal region being seemingly climatically suitable (Tribe & Richardson, 1994). The harsher, drier conditions on the Cape Flats (Fynbos Biome) may have prohibited range expansion beyond the Cape Peninsula (Tribe & Richardson, 1994), although in recent years this species has spread inland to Stellenbosch and as far as the Hottentots Holland mountains. Population numbers also appear to show large annual fluctuations in the Western Cape, although this trend is yet to be quantified (T. Wossler pers. comm., 2010). Although not strictly ground-dwelling, the European wasp is included in this study because of its ground-nesting habit and known impacts on other ground-dwelling invertebrates.

European wasps have injurious effects on both native wasp species and other native arthropods. Evidence for such detrimental impacts comes from semi-urban scrubland-pastures (Harris & Oliver, 1993) and beech forests (Beggs, 2001) in New Zealand. Adult European wasps catch invertebrate prey to meet the requirements of their larvae for fresh protein (Caron & Schaefer, 1986). Diptera, Hymenoptera, Lepidoptera larvae and Araneae are the most common invertebrate prey items taken by European wasps in New Zealand (Harris & Olivier, 1993), Australia (Kasper *et al.*, 2004) and Argentina (Sackmann *et al.*, 2000). Although no equivalent dietary study has been undertaken in South Africa, the most common invertebrate prey items taken are likely to include the same taxa, since these are amongst the most commonly found in nature. This suggests that European wasps are generalist, rather than selective, predators (Sackmann *et al.*, 2000). They also compete with birds for insect food resources, effecting entire insectivorous bird communities in New Zealand (Harris, 1991; Beggs, 2001). In addition to protein prey items, European wasps also forage for water, pulp and carbohydrates (Kasper *et al.*, 2004). Adults collect wood pulp for building nests and require carbohydrates as an energy source (Caron & Schaefer, 1986). Adults mostly feed on nectar, but also pierce soft fruits, such as grapes, pears and plums, compromising soft-fruit and wine industries. By removing large quantities of honeydew (a carbohydrate source), European wasps may alter nutrient cycling by decreasing the flow of carbon to soil microorganisms (Beggs, 2001). Removal of honeydew may have additional indirect effects on the ecosystem and on other invertebrate taxa, such as ants, that also utilize this resource.

Molluscs have received more attention than most other non-insect invertebrate taxa, most often for their notorious economic impacts. Six molluscs, including the terrestrial Giant African snail (*Achatina fulica*) and Rosy wolf snail (*Euglandina rosea*), are among the *100 of the world's worst invasive alien species* (Lowe *et al.*, 2000). Despite severe impacts for agriculture, a long history of invasion (over 150 years for several species), and establishment in relatively

undisturbed natural areas (Herbert, 2010), alien terrestrial molluscs have received inadequate attention in the South African literature, even in reviews discussing alien invertebrates (Lach *et al.*, 2002). Herbert (2010) inventoried the South African alien terrestrial mollusc fauna, listing 34 introduced species, of which 28 have established. Most terrestrial mollusc introductions have taken place in Cape Town, because it is a major port of entry, has a long European colonial history (dating back to the 1600s) and a temperate, Mediterranean climate. Twenty alien mollusc species have been collected in Cape Town – more than all other South African localities combined. Of the 34 introduced terrestrial mollusc species in South Africa, 25 have also invaded southern Australia, which shares a similar Mediterranean climate, and 19 have invaded New Zealand (Smith, 1992; Barker, 1999; Herbert, 2010). This resemblance is not surprising, as both Australia and New Zealand share a comparable colonial history with South Africa.

Since most millipedes are phytophages, saprophages or detritivores, alien millipedes are unlikely to pose a serious threat to native biodiversity and ecosystems (Baker, 1985; Stoev *et al.*, 2010). Some millipedes have, however, attained pest status in their invaded habitats. The Portuguese millipede (*Ommatoiulus moreleti*), native to the Iberian Peninsula, was introduced to Australia in 1953, where it quickly reached “plague proportions” and invaded houses in spring and autumn (McKillup *et al.*, 1988; Stoev *et al.*, 2010). *O. moreleti* numbers typically explode in newly-invaded areas in Australia, then decrease over time, possibly due to food shortages (Baker, 1985), or control by a native rhabditid nematode (McKillup *et al.*, 1988). These “boom and bust” dynamics of invasive alien species have also been reported for terrestrial mammals, aquatic plants and marine invertebrates (reviewed in Parker *et al.*, 1999). *O. moreleti* is also considered a nuisance in South Africa (Lawrence, 1984).

Alien woodlice are largely confined to urban environments, where they often become dominant detritus feeders (Cochard *et al.*, 2010). The ability to rapidly build up large numbers and exploit resources more successfully than native species (Sutton, 1972), means that successful invasion of relatively natural habitats can lead to disturbance (Cochard *et al.*, 2010). *Armadillidium vulgare*, *Porcellionides pruinosus* and *Porcellio scaber* are considered “synanthropically cosmopolitan” woodlice species (Cochard *et al.*, 2010). The Rough woodlouse (*P. scaber*), which originates from southwestern Europe, has colonised the rest of Europe and many other parts of the world, including Africa (Slabber & Chown, 2002). It has been recognised as an invasive alien species in South Africa for many decades (Lawrence, 1953). It also spread from South Africa to Marion Island, probably arriving in building supplies from Cape Town in April 2001 (Slabber & Chown, 2002).

While there have been numerous studies on Argentine ant impacts in South Africa, including a few previous studies on Table Mountain, this study is unique in its direct attempt to inventory the entire community of alien invertebrates and to assess their impacts on native invertebrates on the Cape Peninsula. The first aim of this study is to investigate the impacts of invasive alien Argentine ants on (a) native ants and (b) other invertebrates in Table Mountain National Park. The literature suggests that native ant species richness and abundance will be largely reduced at sites where Argentine ants have invaded (*i.e.* are present), compared to uninvaded sites. Community composition of native ants is also expected to differ between Argentine ant invaded and uninvaded sites, with greater similarity between invaded sites across habitats.

The species richness and abundance of non-ant invertebrates and Cape Peninsula endemics are predicted to be lower at sites where Argentine ants are present than at sites where they are absent. Conversely, the species richness and abundance of alien invertebrates is predicted to be higher at sites invaded by Argentine ants. The impacts of invasion by Argentine ants are predicted to differ between taxa, but generally to be negative, with lower abundance at invaded compared to uninvaded sites. Community composition of non-ant invertebrate, Cape Peninsula endemic and non-ant alien invertebrate species are expected to differ between uninvaded and invaded sites, with greater similarity between sites where Argentine ants are present across habitats, assuming patterns are not confounded by sample size or spatial autocorrelation among sites. Co-occurrence patterns of native ant species are predicted to be nonrandomly segregated at uninvaded sites, but to show community disassembly and a tendency towards random associations at sites where Argentine ants are present. Community disassembly is a change from nonrandom to random co-occurrence of species that alters community organisation, and has been documented in native ant communities as a result of invasion by Argentine ants (Sanders *et al.*, 2003). The impact of Argentine ants on native ants is also expected to differ according to functional group, but is predicted to be negative for most native ant species.

By comparison to Argentine ants, the impacts of the vast majority of alien species have not yet been quantified (Parker *et al.*, 1999). Nevertheless, it is generally assumed that most invasions do have ecological impacts on the invaded ecosystem (Ricciardi & Kipp, 2008), and that these impacts span a skewed continuum in which the most adverse impacts are comparatively rare, *i.e.* the upper tail of a log-normal distribution (Williamson & Fitter, 1996). Thus the second aim of this study is to profile and investigate the impacts of non-ant alien invertebrate species on native ground-dwelling invertebrate species richness, abundance and

community composition in Table Mountain National Park. The identification of potentially high-impact (*sensu* Ricciardi & Kipp, 2008) alien invaders that may be implicated in substantial declines of native invertebrate populations is of scientific interest and urgent conservation concern. Habitat alteration, such as afforestation, may also facilitate such invasions. This is investigated by contrasting alien invertebrate communities in natural and transformed vegetation on the Cape Peninsula.

## Methods

### *Study sites and collecting methods*

Most studies attempting to quantify the impacts of alien species are correlative, either comparing one site before and after invasion, or different sites where the alien species is either present or absent (Parker *et al.*, 1999). However, few Cape Peninsula locality records exist for most of the alien species collected, and many of these records are from many years ago. Hence *a priori* selection of invaded and uninvaded sites was neither possible nor practical. Therefore, this study did not adopt either a before-and-after invasion comparison or direct comparison across a moving invasion front. Instead, this study compared sites assigned after sampling as uninvaded or invaded by Argentine ants (*L. humile*) and 18 other non-ant alien invertebrates in three habitats across one spring-summer season.

Refer to Chapter 2 for the location of sites sampled and collecting methods used in Western Cape Afrotropical Forest (n = 8 sites), Peninsula Sandstone and Granite Fynbos (n = 8 sites) and pine plantation (n = 7 sites; Site 11 omitted) in Table Mountain National Park. For each of the 23 sites, data from the replicates (10 leaf litter, 10 soil, 10 pitfall trap, 10 sugar-baited ant trap and two decayed log samples) were pooled to obtain a single abundance or species richness value per site. Refer to Appendix C for a list of the 670 species collected in forest, fynbos and pine plantation.

### *Analyses*

The region of origin, South African distribution, habitats invaded locally and date of first record of introduction in South Africa were summarised for all the alien invertebrates identified. Since comparatively more is known about Argentine ants than the other alien invertebrates collected, the analyses were split into three sections: Argentine ant impacts on native ants, Argentine ant impacts on other ground-dwelling invertebrates, and other alien invertebrate species impacts on their corresponding native taxa.

*Analyses for impacts of Argentine ants on native ants*

Species-accumulation curves were plotted for the observed species richness of ants in forest, fynbos and pine plantation to ascertain whether assemblages were adequately sampled. Species-accumulation curves were calculated using  $S_{obs}$  Mao Tau sample-based rarefaction curves, randomised 50 times in EstimateS version 8 (Colwell, 2006). The  $x$ -axis of these sample-based rarefaction curves was re-scaled from sites sampled to individuals. Observed ant species richness counts were re-scaled to obtain abundance-standardised ant species richness, using the lowest number of individuals collected at a site. Re-scaling is necessary when curves do not reach an asymptote and/or there is overlap in the 95% confidence intervals, because individual densities vary among samples and species rich invertebrate communities are impractical to sample exhaustively (Gotelli & Colwell, 2001; Colwell *et al.*, 2004).

Mean ( $\pm$  SD) species richness and abundance of native ants were calculated at sites uninvaded and invaded by Argentine ants in STATISTICA version 9 (StatSoft, Inc., 2009). Sites were scored as “uninvaded” if Argentine ants were absent and “invaded” if Argentine ants were present. Species richness and abundance of native ants in each habitat were compared for sites uninvaded and invaded by Argentine ants using Mann-Whitney  $U$  tests in STATISTICA. Native ant species richness was regressed against Argentine ant abundance at sites in each habitat, to test the prediction that native ant species richness is reduced when Argentine ants are highly abundant.

Impacts of Argentine ant invasion on native ant species were investigated by comparing the mean ( $\pm$  SD) abundance of each native ant species between uninvaded and invaded sites. Impacts were scored by calculating the percentage change in abundance with invasion. Impacts were scored as “positive” if there was an increase in mean abundance with invasion, “negative” if there was a decrease in mean abundance with invasion, and “0” if an ant species was not collected at any site in that habitat.

A Bray-Curtis dissimilarity matrix of fourth-root transformed community composition between sites was used to map the interrelationships of native ant communities in cluster analysis by group average clustering, and in ordination by non-metric multidimensional scaling (MDS), in PRIMER version 6 (Clarke & Gorley, 2006). Data were fourth-root transformed to down-weight highly abundant species. In an MDS plot, the  $x$ -axis represents the direction of maximum variation, with the position of samples (or sites in this case) reflecting compositional similarity. The stress value acts as a measure of reliability, since the risk of drawing false inferences from an ordination increases with greater stress. Stress values less than 0.2 are



deemed reliable. Clusters on the MDS plot were overlaid from the resemblance levels (*i.e.* the percentage similarity) obtained from the dendrogram plot in PRIMER.

The same Bray-Curtis dissimilarity matrix of native ant data was used for pairwise analysis of similarity (ANOSIM), to test the null hypothesis of no difference in ant community composition between sites uninvaded and invaded by Argentine ants in each habitat. ANOSIM is the non-parametric, multivariate equivalent of ANOVA, applied to the rank dissimilarity matrix using a permutation procedure (999 permutations) (Clarke & Green, 1988). It calculates the *R* statistic, which provides a relative measure of separation of predefined groups, and ranges from zero (no difference among groups) to one (all samples within groups are more similar to one another than to any samples from another group). ANOSIM was used here to confirm whether the cluster pattern identified in the ordination was statistically significant.

Co-occurrence patterns of native ant species were compared between sites uninvaded and invaded by Argentine ants in each habitat, using Stone & Roberts' (1990) *C*-score index, calculated with EcoSim 7.72 simulation software (Gotelli & Entsminger, 2010). Co-occurrence analyses use a presence-absence data matrix to test for nonrandom patterns of species co-occurrence, based on a null model algorithm (Sanders *et al.*, 2003). In each matrix, rows represent species, columns represent sites, and the entries are the presence (1) or absence (0) of a species at a site. The *C*-score index quantifies the average number of "checkerboard units" found between all species pairs, where a checkerboard unit is a 2 x 2 submatrix of the form 0 1, 1 0 or 1 0, 0 1 (Sanders *et al.*, 2003). For each pair of species, the *C*-score was calculated as  $(R_i - S)(R_j - S)$ , where  $R_i$  and  $R_j$  are the matrix row totals for species *i* and *j*, and *S* is the number of sites where both species occur (Stone & Roberts, 1990). Each observed data matrix was randomised 5000 times using a null model, with fixed sums of rows and equiprobable columns, to calculate the expected *C*-score. If a community is structured by competitive species interactions, then its *C*-score should be significantly larger than expected by chance (Gotelli, 2000; Gotelli & McCabe, 2002). The standardised effect size (SES) was also calculated for each matrix, by measuring the number of standard deviations that the observed index is above or below the mean simulated (*i.e.* expected) index (Gotelli & McCabe, 2002). SES values in the range of 2.0 to -2.0 approximate the 5% significance level, and may be interpreted as random community associations. SES values greater than 2.0 suggest nonrandom segregation, while values less than -2.0 suggest nonrandom aggregation in the community.

Ant functional groups for the genera collected, and their responses to Argentine ants, were extracted from the literature. Functional groups were also expressed as a proportion of the total number of native species and mean individuals collected in uninvaded and invaded sites in

each habitat, to establish whether Argentine ant presence-absence impacted native ant assemblages, based on their niche dimensions. Abundance was standardised by site because of unequal sample sizes (number of sites). Species richness and abundance of native ants in each functional group in each habitat were compared for sites where Argentine ants were present and absent using Mann-Whitney *U* tests in STATISTICA.

*Analyses for impacts of Argentine ants on other invertebrates*

Mean ( $\pm$  SD) species richness and abundance of all non-ant invertebrates, Cape Peninsula endemics and non-ant alien invertebrates were compared between sites where Argentine ants were present (invaded) and absent (uninvaded) in each habitat. Mann-Whitney *U* tests were used to compare the species richness and abundance of all non-ant invertebrates, Cape Peninsula endemics and non-ant alien invertebrates between sites uninvaded and invaded by Argentine ants in each habitat in STATISTICA.

Impacts of invasion by Argentine ants on non-ant, Cape Peninsula endemic and other alien invertebrates were investigated by comparing the mean ( $\pm$  SD) abundance of each taxon (for all invertebrates) or species (for endemics and aliens) between uninvaded and invaded sites. Impacts were scored by calculating the percentage change in abundance with invasion. Impacts were scored as “positive” if there was an increase in mean abundance with invasion, “negative” if there was a decrease in mean abundance with invasion, “neutral” if there was no difference in mean abundance with invasion, and “0” if a species was not collected at any site.

Bray-Curtis dissimilarity matrices of fourth-root transformed community composition between sites were used to map the interrelationships of all, endemic and alien invertebrate communities in ordination by non-metric multidimensional scaling (MDS), in PRIMER. Pairwise analysis of similarity (ANOSIM) was used to test the null hypothesis of no difference in the community composition of all, endemic and alien invertebrates with invasion in each habitat. For endemics, pine plantation sites were omitted from the MDS ordination and ANOSIM, because only one endemic species (*Uroplectes insignis*) was collected at Sites 2 and 4, and no endemic species was collected at the other five pine plantation sites sampled.

*Analyses for impacts of other alien species on their corresponding native taxa*

For non-ant alien invertebrates, each alien species was compared to its corresponding native taxon only (e.g. Portuguese millipede compared to native millipede species), because impacts due to competition or predation (cannibalism in the case of some molluscs) were expected to be most evident among taxonomically related species. The impacts of other alien invertebrates,

some of which were identified to morphospecies only, were not applied to their corresponding functional groups, because of the difficulty in accurately assigning morphospecies to functional groups. Sites were scored as “uninvaded” if the alien species in question was absent and “invaded” if the alien species was present. Non-parametric analyses were used for all alien species collected, because residuals of data were not normally distributed for most alien species, and abundance and incidence were generally quite low.

Spearman rank correlations were calculated for all habitats combined, and for each habitat, to establish whether the abundance of each alien species was significantly associated with the species richness and abundance of native species from the alien’s associated taxon. Mean ( $\pm$  SD) native species richness and abundance were calculated between sites where each alien was present and absent in each habitat, and then compared using Mann-Whitney *U* tests, to establish whether observed impacts were statistically significant. Several alien species were collected at one site only, so comparisons of mean native species richness and abundance were not made for these species. All species richness and abundance comparisons were performed in STATISTICA.

A triangular matrix of Bray-Curtis dissimilarity of fourth-root transformed community composition between sites was used to map the interrelationships of invertebrate communities for each alien invertebrate species’ corresponding taxon in cluster analysis, using group average clustering, and in ordination by non-metric multidimensional scaling (MDS), in PRIMER. Sites with no corresponding native species collected in that taxon were omitted. The same dissimilarity matrices were used for ANOSIM, to test the null hypothesis of no difference in community composition between sites for each alien species presence-absence. ANOSIM was applied to the rank similarity matrix using a permutation procedure (999 permutations) to test for statistical significance of the cluster patterns identified in the ordinations.

## Results

Nineteen alien invertebrate species were collected in forest, fynbos and pine plantation. The invasion history and currently known South African distribution of these alien invertebrate species were summarised from the literature (Table 4.1). The Argentine ant was the only alien species to have originated from the Southern Hemisphere. All alien molluscs identified were European in origin, with most species from the Mediterranean region. Most alien mollusc species have been established in South Africa for many decades (and some perhaps for centuries), and several have distributions beyond the Western Cape Province. The Portuguese

millipede, Rough woodlouse, springtails and European wasp all have a Palearctic (mostly European) native range, and most have a synanthropically cosmopolitan distribution. The South African distribution and habitats invaded by alien invertebrates (other than ants and molluscs) have not yet been adequately studied, but distribution maps for some species have recently become available (Picker & Griffiths, 2011).

**Table 4.1.** Invasion history of alien invertebrates collected, excluding those lacking positive species-level determinations.

Species	Common names	Native range	South African distribution	South African habitats invaded	Date introduced	References <sup>+</sup>
<i>Linepithema humile</i> *	Argentine ant	Paraná River basin in subtropical South America	Six of the nine provinces	Agricultural, urban, plantation and natural areas	Prior to 1901	Prins <i>et al.</i> , 1990; Wild, 2004; Luruli, 2007
<i>Arion hortensis</i> aggregate <sup>#</sup>	Garden arion, Férussac's orange-soled slug, Yellow-soled slug	Western Europe	Cape Town and Stellenbosch	Exotic pine plantations	Prior to 1939	Herbert, 2010
<i>Deroceras panormitanum</i> *	Brown field slug, Long-necked field slug	Probably Mediterranean	Western Cape, Eastern Cape and Gauteng	Suburban and rural gardens, forest on Table Mountain and near Somerset East	Prior to 1963	Herbert, 2010
<i>Lehmannia valentiana</i>	Three-banded garden slug, Valencia slug	Iberian Peninsula	Western Cape, Eastern Cape, Northern Cape, KwaZulu-Natal and Kruger National Park	Suburban and rural gardens, and natural habitats in Cape Town	Prior to 1961	Herbert, 2010
<i>Limax maximus</i>	Giant garden slug, Great grey slug, Tiger slug, Leopard slug, Spotted garden slug	Western and Central Europe, and perhaps North Africa	Western Cape	Cape Town: forest near suburbia and on Table Mountain	Prior to 1898	Herbert, 2010
<i>Cochlicopa</i> cf. <i>lubricella</i>	Slender moss snail	Holarctic	Western Cape, Eastern Cape, Gauteng and North West Province	Primarily in gardens, Kirstenbosch and Knysna forest	Prior to 1965	Herbert, 2010
<i>Vitrea contracta</i>	Milky crystal snail, Contracted glass snail	Much of Europe, Ukraine, Turkey, Caucasia, Middle East and North Africa	East facing slopes of Table Mountain and Cape Peninsula	East-facing slopes on Cape Peninsula, and probably more widely distributed in Cape Town and surrounds	Prior to 2004, probably not recent	Herbert, 2010
<i>Cornu aspersum</i>	Brown garden snail, Common garden snail	Western Europe and the Mediterranean	All nine provinces, synanthropic and not widespread in natural habitats	Most widespread alien terrestrial snail in South Africa	Prior to 1878, probably much earlier	Herbert, 2010

Species	Common names	Native range	South African distribution	South African habitats invaded	Date introduced	References <sup>+</sup>
<i>Lauria cylindracea</i>	Common chrysalis snail	Western Europe and the Mediterranean	Cape Town, Cape Peninsula and Worcester	Gardens, vineyards and exotic conifer plantations	Prior to 1879	Herbert, 2010
<i>Oxychilus draparnaudi</i> *	Draparnaud's glass snail, Dark-bodied glass snail	Western Europe and the Mediterranean	Western Cape, Eastern Cape, Northern Cape and Gauteng	Spread into native habitats and abundant on Table Mountain above Newlands and Kirstenbosch	Circa 1908, or earlier	Herbert, 2010
<i>Ommatoiulus moreleti</i>	Portuguese millipede	Iberian Peninsula	Cape Town and the South Western Cape	Gardens, pine plantations and Afrotropical forest	Prior to 1984, probably much earlier	Lawrence, 1984; Hamer, 1998
<i>Porcellio scaber</i>	Rough woodlouse	South Western Europe	Cape Town, and probably widespread across the country	Gardens and Afrotropical forest	Prior to 1885	Barnard, 1932; Lawrence, 1953; Slabber & Chown, 2002
<i>Entomobrya nivalis</i>	springtail	Palaearctic	Not adequately studied	Not known	Prior to 1934	Womersley, 1934; Paclt, 1956.
<i>Neanura muscorum</i>	springtail	Palaearctic	Not adequately studied	Not known	Prior to 1968	Coates, 1968
<i>Tomocerus minor</i>	springtail	Palaearctic	Not previously recorded	Not previously recorded	Post 1956	Womersley, 1934; Paclt, 1956; E. Bernard pers. comm., 2010
<i>Vespula germanica</i> *	European wasp, German wasp, Yellowjacket	Eurasia and North Africa	Cape Peninsula, Stellenbosch, Somerset West, to Hottentots-Holland Mountains	Afrotropical forest, Fynbos, orchards and vineyards	Prior to 1970	Whitehead & Prins, 1975; Richardson <i>et al.</i> , 1992; Tribe & Richardson, 1994; T. Wossler pers. comm., 2010

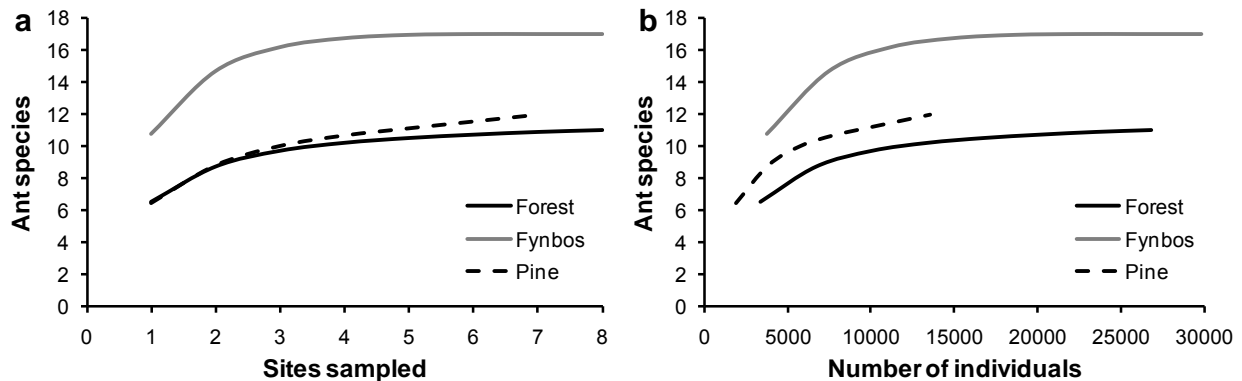
<sup>+</sup> For further reference to the distribution and date of introduction of many of these species, see Picker & Griffiths (2011)

\* Cannibal or carnivorous species

# *Arion hortensis* aggregate is a member of an unresolved species complex

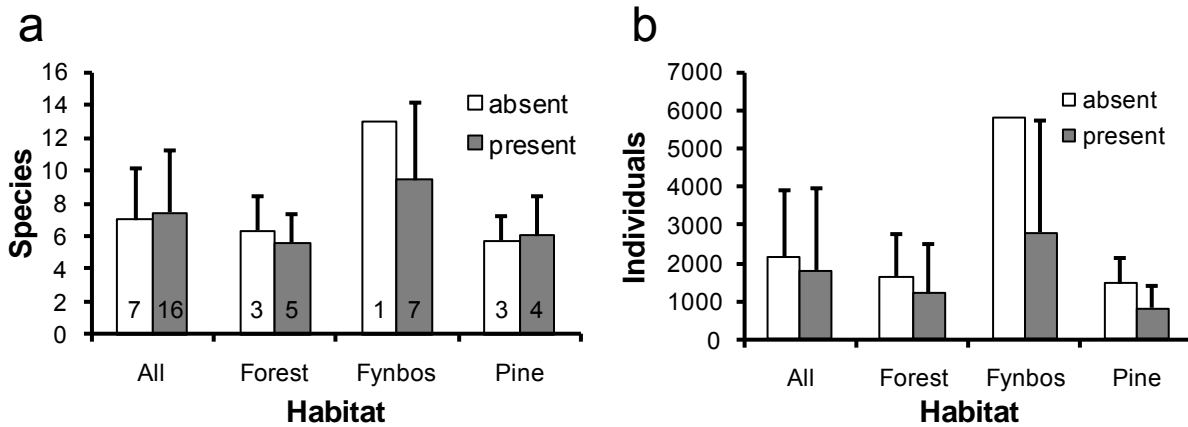
*Argentine ants and native ants*

Seventeen ant species were collected in forest (11 species), fynbos (17) and pine plantation (12). Sampling achieved saturation in fynbos, and closely approached saturation in both forest and pine plantation (Fig. 4.1a). Re-scaling of the x-axis of sample-based rarefaction curves from sites sampled to individuals (Fig. 4.1b) retained fynbos as the habitat with the highest observed ant species richness. This pattern held with an abundance-standardised comparison of 13 409 individuals, based on the lowest total ant abundance, recorded in forest.



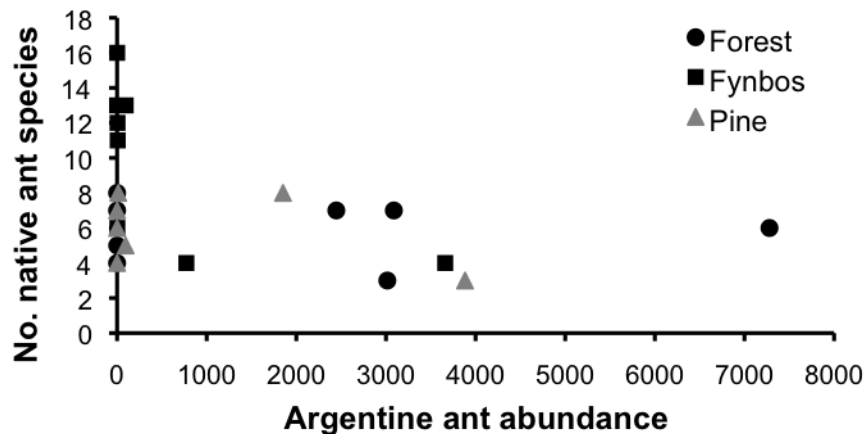
**Figure 4.1.** Sample-based rarefaction curves of observed ant species richness in forest, fynbos and pine plantation with (a) number of sites sampled and (b) number of individuals. Curves were calculated using  $S_{obs}$  Mao Tau and randomised 50 times. The sample-based rarefaction curves were re-scaled to number of individuals, because the pine plantation curve did not reach an asymptote and the 95% confidence intervals for forest and pine plantation overlapped.

Argentine ants were present at 16 of the 23 sites sampled and in all three habitats. Mean native ant species richness was not different under Argentine ant invasion (Fig. 4.2a). Mean ( $\pm$  SD) native abundance was slightly, but not significantly, higher in uninvaded sites, due to high variance among sites (Fig. 4.2b). None of the habitats differed significantly (Mann Whitney  $U$  tests,  $p > 0.05$ ) in native species richness or abundance with Argentine ant invasion.



**Figure 4.2.** Mean (a) species richness and (b) abundance of native ants under Argentine ant presence-absence. The number in each bar (a) is the number of sites used in calculations. Error bars reflect the (positive) standard deviation associated with means.

No linear relationship was found between Argentine ant abundance and native ant species richness in either forest ( $F_{1,6} = 0.015$ ,  $R^2 = 0.002$ ,  $p = 0.908$ ), fynbos ( $F_{1,6} = 3.912$ ,  $R^2 = 0.395$ ,  $p = 0.953$ ) or pine plantation ( $F_{1,5} = 0.991$ ,  $R^2 = 0.165$ ,  $p = 0.365$ ) (Fig. 4.3). Neither could the relationship between Argentine ant abundance and native ant species richness be described as unimodal (quadratic) in forest ( $F_{2,5} = 0.176$ ,  $R^2 = 0.066$ ,  $p = 0.844$ ), fynbos ( $F_{2,5} = 2.604$ ,  $R^2 = 0.510$ ,  $p = 0.168$ ) or pine plantation ( $F_{2,4} = 0.134$ ,  $R^2 = 0.720$ ,  $p = 0.079$ ). None of these relationships were significant ( $p > 0.05$ ), possibly due to the uneven spread in Argentine ant abundance, high habitat heterogeneity and low number of sites sampled in each habitat.



**Figure 4.3.** Relationship between Argentine ant abundance and native ant species richness.

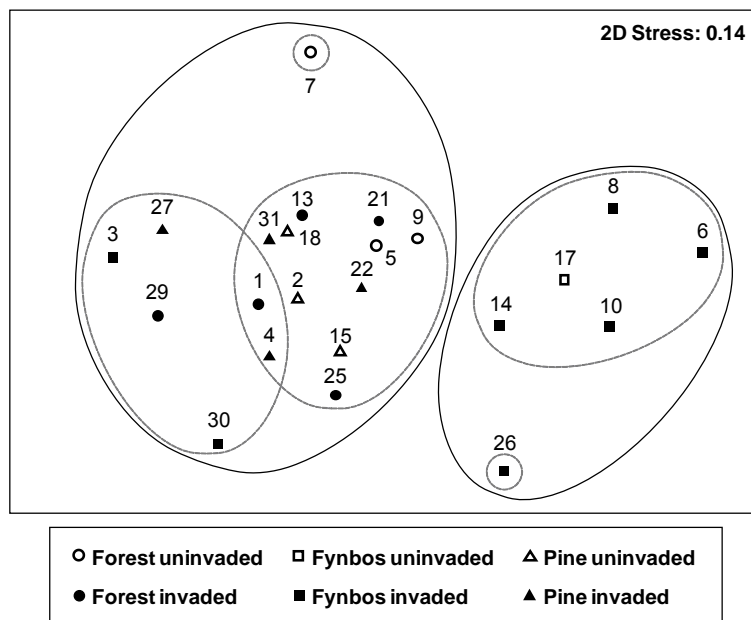


The impacts of Argentine ants on individual native ant species were not consistent across habitats and could not be clearly determined (Table 4.2). Several ant species were collected from only a few sites. For example, *Meranoplus* sp. appears to be negatively impacted by the presence of Argentine ants in forest and pine plantation, but was in fact collected from only one site each in forest and pine plantation, thus refuting the possible negative impact. Furthermore, the variance in mean abundance between sites where Argentine ants were present and absent was high, most likely reflecting incidental or naturally patchy distributions, rather than any consequence of Argentine ant invasion. Sample sizes (*i.e.* number of sites) may also be generally too low to produce statistically meaningful results. Even when a change of 100% or more was recorded, this was often for only a few individuals and therefore not really meaningful for ant species that live in colonies. Impacts in fynbos were particularly difficult to identify, because Argentine ants were absent from only one fynbos site sampled.

**Table 4.2.** Impacts of invasion by Argentine ants on the mean  $\pm$  SD abundance of native ant species collected. Impacts were scored as “positive” if there was an increase in mean abundance with invasion (presence), “negative” if there was a decrease in mean abundance with invasion, and “0” if a species was not collected at any site in that habitat. n = number of sites. % = percentage change in abundance with invasion. \* = absent in uninvaded.

Native ant species	Forest				Fynbos				Pine plantation			
	Absent (n = 3)	Present (n = 5)	Impact	%	Absent (n = 1)	Present (n = 7)	Impact	%	Absent (n = 3)	Present (n = 4)	Impact	%
<i>Tapinoma</i> sp.	0	0	0		5	107.4 $\pm$ 237.8	positive	2048.57	0	66.3 $\pm$ 132.5	positive	*
<i>Technomyrmex pallipes</i>	0	0	0		23	186.0 $\pm$ 377.6	positive	708.70	0	3.3 $\pm$ 6.5	positive	*
<i>Camponotus bertolinii</i>	2.3 $\pm$ 3.2	9.4 $\pm$ 19.4	positive	302.86	1	52.9 $\pm$ 115.2	positive	5158.71	40.0 $\pm$ 69.3	7.3 $\pm$ 10.7	negative	-81.88
<i>Camponotus niveosetosus</i>	6.0 $\pm$ 7.9	3.6 $\pm$ 4.5	negative	-40.00	126	88.0 $\pm$ 162.4	negative	-30.16	1.0 $\pm$ 1.0	2.3 $\pm$ 3.3	positive	125.00
<i>Camponotus</i> sp. 1	0	0	0		1	52.9 $\pm$ 64.6	positive	5158.71	0	0	0	
<i>Camponotus</i> sp. 2	185.0 $\pm$ 251.6	8.0 $\pm$ 12.0	negative	-95.68	2930	204.3 $\pm$ 346.7	negative	-93.03	4.0 $\pm$ 4.0	27.8 $\pm$ 54.8	positive	593.75
<i>Lepisiota capensis</i>	1.3 $\pm$ 1.2	0.2 $\pm$ 0.4	negative	-85.00	0	1291.4 $\pm$ 2876.6	positive	*	1.7 $\pm$ 1.5	5.0 $\pm$ 10.0	positive	200.00
<i>Crematogaster</i> sp.	233.7 $\pm$ 317.4	21.0 $\pm$ 45.3	negative	-91.01	1630	262.1 $\pm$ 442.1	negative	-83.92	0	0	0	
<i>Meranoplus</i> sp.	93.7 $\pm$ 162.2	0	negative	-100.00	0	67.7 $\pm$ 96.1	positive	*	0	0	0	
<i>Monomorium</i> sp.	616.3 $\pm$ 706.9	248.0 $\pm$ 196.2	negative	-59.76	393	71.1 $\pm$ 118.4	negative	-81.90	1134.0 $\pm$ 665.1	469.0 $\pm$ 437.4	negative	-58.64
<i>Myrmicaria nigra</i>	0	0	0		19	37.9 $\pm$ 96.3	positive	99.25	0	0	0	
<i>Pheidole capensis</i>	0	0	0		2	220.4 $\pm$ 377.7	positive	10921.43	0	0	0	
<i>Tetramorium grassii</i>	517.0 $\pm$ 396.2	488.6 $\pm$ 790.0	negative	-5.49	478	88.7 $\pm$ 184.3	negative	-81.44	247.7 $\pm$ 119.0	236.0 $\pm$ 172.2	negative	-4.71
<i>Tetramorium</i> sp.	0	421.8 $\pm$ 942.6	positive	*	51	38.3 $\pm$ 68.8	negative	-24.93	41.7 $\pm$ 71.3	1.5 $\pm$ 1.9	negative	-96.40
<i>Hagensia peringueyi</i>	0	0	0		127	17.9 $\pm$ 37.3	negative	-85.94	0	0	0	
<i>Tetraoponera</i> sp.	2.3 $\pm$ 2.5	2.8 $\pm$ 5.2	positive	20.00	0	5.3 $\pm$ 10.8	positive	*	1.0 $\pm$ 1.7	4.5 $\pm$ 2.4	positive	350.00

Native ant community composition varied between habitats. In an MDS ordination of native ant species (Fig. 4.4), sites clustered in two broad groups, with 37% similarity between them. One cluster contained all undisturbed Granite and Sandstone Fynbos sites. Site 26 (Sandstone Fynbos) was spatially separated from other mature fynbos sites, possibly reflecting some unknown difference between Tokai (Silvermine Mountain) and Table Mountain. The other primary cluster contained both recovering fynbos sites (Sites 3 and 30, previously under pine) and all forest and pine plantation sites. Even at 49% similarity (smaller circles on MDS plot), there was no clear separation of forest from pine plantation sites, or across a north-south spread of localities. Although Site 7 (forest in Kirstenbosch) appeared to be an outlier (spatially separated from other forest sites on the MDS plot), it was retained in the analysis, because there was no reason to believe that collector bias, adverse weather conditions or other confounding variables were responsible for the very low ant abundance and low number of ant species collected there. There was no clear separation of sites in any habitat based on the presence of Argentine ants.



**Figure 4.4.** Ordination from non-metric multidimensional scaling (MDS), applied to a Bray-Curtis dissimilarity matrix of fourth-root transformed community composition amongst sites for native ants. Numbers refer to sites (see Appendix A) and symbols to Argentine ant presence-absence in each habitat. Large black circles represent 37% similarity among sites, and smaller grey circles 49% similarity.

ANOSIM confirmed the pattern observed in the ordination (Fig. 4.4). ANOSIM showed that the native ant community did not differ significantly between sites uninvaded and invaded by Argentine ants within habitats, between invaded sites across habitats, or between uninvaded sites across habitats (Table 4.3). Pairwise ANOSIM test results, such as pine invaded versus forest uninvaded, that had no direct relevance to the null hypothesis, were omitted. None of these omitted ANOSIM results were significant ( $p < 0.05$ ).

**Table 4.3.** ANOSIM for native ant community composition at sites uninvaded and invaded by Argentine ants in each habitat. Significance set at  $p < 0.05$ .

<b>Habitat pairs</b>	<b><i>R</i></b>	<b><i>p</i></b>
Forest invaded vs. Forest uninvaded	0.108	0.304
Fynbos invaded vs. Fynbos uninvaded	-0.197	0.750
Pine invaded vs. Pine uninvaded	-0.074	0.571
Forest invaded vs. Fynbos invaded	0.272	0.054
Forest invaded vs. Pine invaded	-0.106	0.738
Fynbos invaded vs. Pine invaded	0.172	0.127
Forest uninvaded vs. Fynbos uninvaded	0.111	0.500
Forest uninvaded vs. Pine uninvaded	0.111	0.300
Fynbos uninvaded vs. Pine uninvaded	1.000	0.250

There was no evidence for community co-occurrence in forest sites, regardless of Argentine ant presence-absence, because the *C*-scores (absent: 0.417 and present: 0.694) were not significantly higher than expected by chance (Table 4.4). Similarly, there was no evidence for co-occurrence in pine plantation sites where Argentine ants were absent. At sites where Argentine ants were present in fynbos and pine plantation, significant *C*-scores (fynbos present: 1.208 and pine present: 0.178) with standardised effect sizes (SES) below -2.0, assuming a normal distribution of standard deviations, were recorded (Table 4.4). This suggests nonrandom co-occurrence (aggregation) in the native ant communities in fynbos and pine plantation under Argentine ant invasion.

**Table 4.4.** Co-occurrence of native ant species at sites uninvaded and invaded by Argentine ants. Observed = observed *C*-score index, Expected = mean of the simulated *C*-score indices, and SES = standardised effect size. Values in bold are significant ( $p < 0.05$ ).

<b>C-score</b>	<b>Observed</b>	<b>Expected</b>	<b><math>p</math> (observed <math>\leq</math> expected)</b>	<b><math>p</math> (observed <math>\geq</math> expected)</b>	<b>SES</b>
<b>Forest</b>					
absent	0.417	0.390	0.626	0.613	0.340
present	0.694	0.856	0.200	0.841	-0.879
<b>Fynbos</b>					
absent	*				
present	1.208	2.490	<b>0.000</b>	1.000	-6.700
<b>Pine plantation</b>					
absent	0.444	0.010	0.751	0.366	0.563
present	0.178	0.454	<b>0.023</b>	0.990	-2.652

\*Omitted because Argentine ants were absent at only one site in fynbos

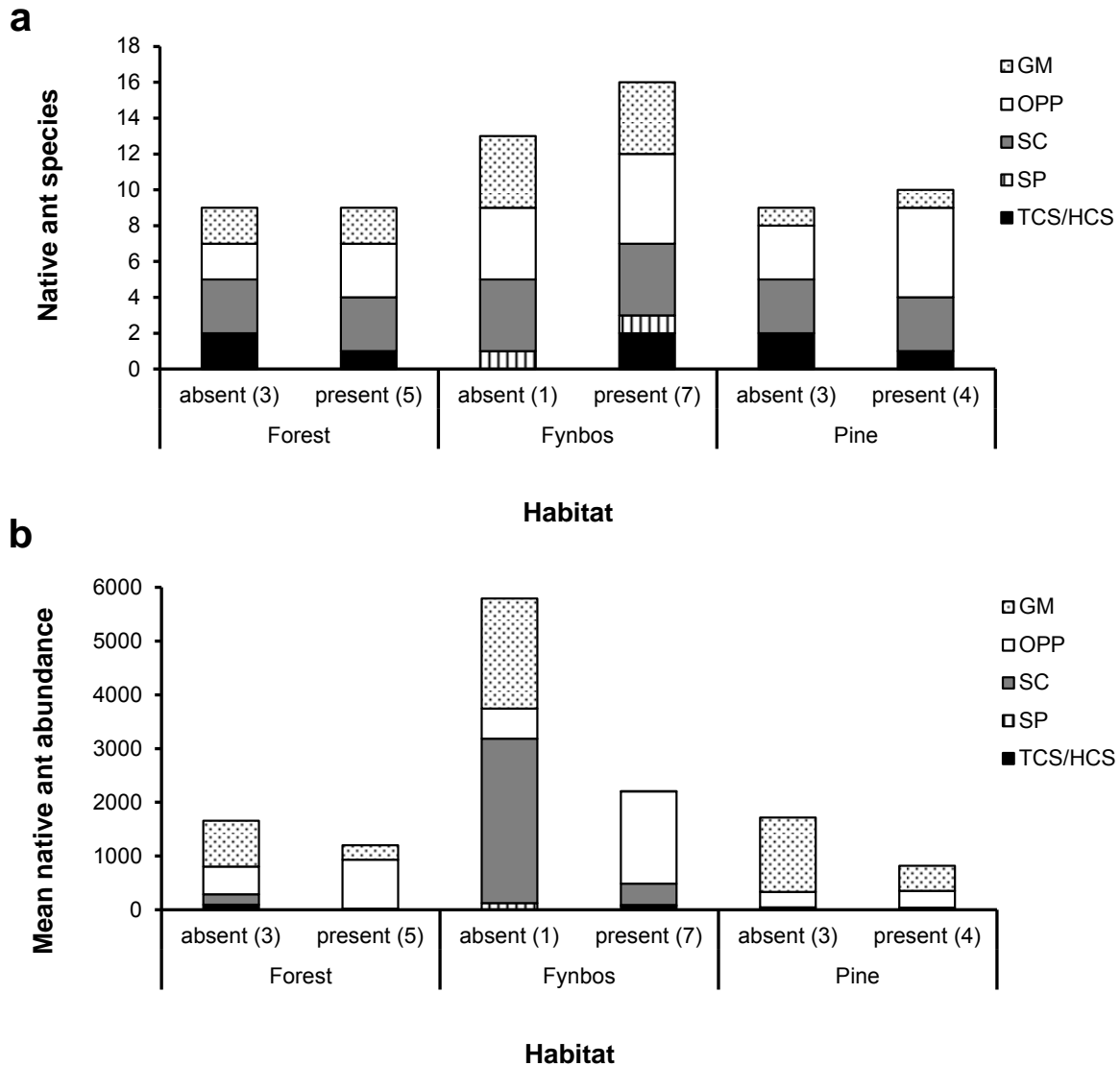
The 17 ant species (in 13 genera) collected were divided among seven functional groups and vary in their known responses to Argentine ants (Table 4.5). The proportions of species in each functional group differed with Argentine ant presence-absence in each habitat (Fig. 4.5a). For Generalized Myrmicinae and Subordinate Camponotini, the same number of species was recorded between sites where Argentine ants were present and absent in each habitat. Opportunists had fewer species at sites where Argentine ants were absent in each habitat. Climate Specialists (Hot Climate Specialists and Tropical Climate Specialists) had more species at sites where Argentine ants were absent in both forest and pine plantation. Fynbos was notably the only habitat to support the Specialist Predators functional group, represented by *Hagensia*, with the single species recorded irrespective of Argentine ant presence-absence. Fynbos also supported all other functional groups and native ant species. Species richness of native ants in each habitat did not differ significantly (Mann-Whitney *U* tests,  $p > 0.05$ ) with Argentine ant presence-absence in any functional group.

The proportions of mean number of individuals in each ant functional group differed with Argentine ant presence-absence in each habitat (Fig. 4.5b). Mean abundance of Generalized Myrmicinae and Subordinate Camponotini was greater at sites where Argentine ants were absent in all habitats. Mean abundance of Specialist Predators was also greater at sites where Argentine ants were absent in fynbos. Opportunists had more individuals on average at sites where Argentine ants were present in each habitat. Climate Specialists (Hot Climate Specialists

and Tropical Climate Specialists) had higher mean abundance with Argentine absence in forest, but with Argentine ant presence in fynbos and pine plantation. Abundance of native ants in each habitat did not differ significantly ( $p > 0.05$ ) with Argentine ant presence-absence in any functional group.

**Table 4.5.** Ant functional groups and their response to the Argentine ant (*Linepithema humile*), based on supporting literature. Functional groups (Andersen, 1997a): DD = Dominant Dolichoderinae, GM = Generalized Myrmicinae, OPP = Opportunists, SC = Subordinate Camponotini, SP = Specialist Predators, HCS = Hot Climate Specialists and TCS = Tropical Climate Specialists.

Genus	Foraging habits	Functional group	Competitive response (at the generic level)	References
<b>Dolichoderinae</b>				
<i>Linepithema</i>	mostly epigaeic	DD	Abundant, active and aggressive. Strong competitive influence over other ants.	Andersen, 1997a
<i>Tapinoma</i>	epigaeic	OPP	Subordinate behaviour.	Majer <i>et al.</i> , 2004
<i>Technomyrmex</i>	epigaeic	OPP	Subordinate behaviour.	Majer <i>et al.</i> , 2004
<b>Formicinae</b>				
<i>Camponotus</i>	epigaeic	SC	Behaviourally submissive to <i>L. humile</i> .	Hoffmann & Andersen, 2003
<i>Lepisiota</i>	epigaeic	OPP	May be able to resist invasions by <i>L. humile</i> .	Edge <i>et al.</i> , 2008
<b>Myrmicinae</b>				
<i>Crematogaster</i>	arboreal	GM	Forage on tree trunks, so little direct interaction with <i>L. humile</i> .	Brown, 2000
<i>Meranoplus</i>	epigaeic	HCS	Occurs where <i>L. humile</i> is not dominant.	Andersen, 2000
<i>Monomorium</i>	epigaeic	GM	Chemical secretions used to repel attacks by <i>L. humile</i> .	Holway, 1999
<i>Myrmecaria</i>	epigaeic	GM	In habitats with low abundance of <i>L. humile</i> .	Majer <i>et al.</i> , 2004
<i>Pheidole</i>	epigaeic	GM	Similar resource requirements to <i>L. humile</i> .	Christian, 2001
<i>Tetramorium</i>	epigaeic	OPP	Coexist with <i>L. humile</i> . Opportunist and defend nest entrances against attack.	Hoffmann & Andersen, 2003
<b>Ponerinae</b>				
<i>Hagensia</i>	epigaeic	SP	Specialist diet, large body size and small colony. Little interaction with other ants.	Andersen, 1997a
<b>Pseudomyrmicinae</b>				
<i>Tetraoponera</i>	arboreal	TCS	Occurs where DD generally not abundant.	Andersen, 1997a

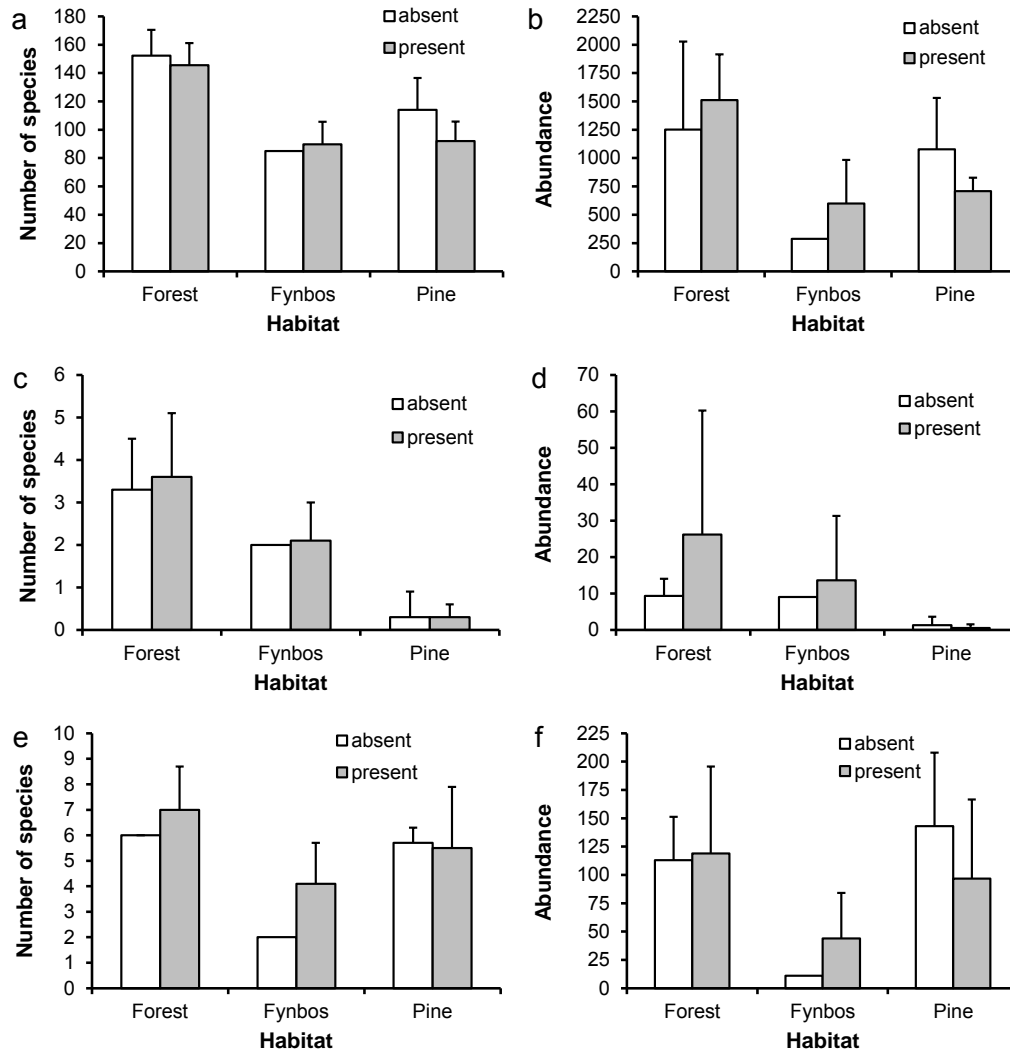


**Figure 4.5.** Functional groups expressed (a) as a proportion of the total number of native ant species and (b) as a proportion of the mean number of native ant individuals collected at sites where Argentine ants were present and absent in each habitat. Number of sites in parentheses. Functional groups: GM = Generalized Myrmicinae, OPP = Opportunists, SC = Subordinate Camponotini, SP = Specialist Predators, HCS = Hot Climate Specialists and TCS = Tropical Climate Specialists.

*Argentine ants and other invertebrates*

In total, 21 866 individuals from 653 non-ant invertebrate species were collected at the 23 sites sampled. Of these, 7276 individuals ( $1039.5 \pm 480.1$  individuals per site) and 564 species were collected at sites where Argentine ants were absent. By comparison, 14 590 individuals ( $911.9 \pm 611.9$ ) and 400 species were collected at sites where Argentine ants were present. Mean species richness and abundance differed across habitats. Mean ( $\pm$  SD) species richness (Fig. 4.6a) and abundance (Fig. 4.6b) of all non-ant invertebrates were not clearly or consistently lower when Argentine ants were present. Contrary to prediction, mean abundance of other invertebrates was slightly higher in both forest and fynbos sites where Argentine ants were present (Fig. 4.6b), but not so in pine plantation sites. For Cape Peninsula endemic invertebrates, mean ( $\pm$  SD) species richness (Fig. 4.6c) and abundance (Fig. 4.6d) were slightly higher in both forest and fynbos sites where Argentine ants were present, again contrary to prediction. For other alien invertebrates, mean ( $\pm$  SD) species richness (Fig. 4.6e) and abundance (Fig. 4.6f) were slightly higher in both forest and fynbos sites where Argentine ants were present, as predicted, but not so in pine plantation. Species richness and abundance of all non-ant invertebrates, Cape Peninsula endemic invertebrates and non-ant alien invertebrates did not differ significantly (Mann-Whitney  $U$  tests,  $p > 0.05$ ) with Argentine ant presence-absence between sites in each habitat. This may be attributed to the low number of sites sampled in each habitat and high variance among sites.





**Figure 4.6.** Mean species richness and abundance of (a and b) non-ant invertebrates, (c and d) Cape Peninsula endemics and (e and f) other alien invertebrates at sites where Argentine ants were absent (uninvaded) and present (invaded). Error bars reflect the (positive) standard deviation associated with means.

The impact of Argentine ants on non-ant invertebrates differed among the 32 invertebrate taxa collected and across habitats (Table 4.6). A few more positive ( $n = 16$ ) than negative ( $n = 11$ ) impacts were observed in forest. Similarly, more positive ( $n = 21$ ) than negative ( $n = 8$ ) impacts were observed in fynbos. However, fewer positive ( $n = 10$ ) than negative ( $n = 18$ ) impacts were observed in pine plantation. Soft-bodied taxa (velvet worms, flatworms, earthworms, slugs, snails and springtails) did not show a consistent trend of more negative impacts of Argentine ants across habitats, and did not have lower mean abundance in

the habitats where Argentine ants were most common. Centipedes and millipedes both showed positive impacts in forest and negative impacts in pine plantation, but opposite impacts in fynbos. Crustaceans were either absent or showed a positive impact of Argentine ants. Arachnids showed more positive than negative associations in all habitats. For insects, impacts varied among orders and habitats, with a similar split in forest and slightly more positive impacts in fynbos, but far more negative impacts in pine plantation. For beetles, bugs, cockroaches, crickets, earwigs, flies, psocids and wasps, there was an equal split in the number of positive and negative impacts in forest, but more positive impacts in fynbos and more negative impacts in pine plantation. The remaining insect orders were collected in low numbers, and represented by only one or two species, often reflecting incidental catches.

The impacts of Argentine ants on Cape Peninsula endemic invertebrates differed among species and across habitats, with more positive than negative impacts recorded (Table 4.7). Habitat specialists, such as the two cockroach species (*Diptertrum brinckae* and *Hoplophoropyga unicolor*) restricted to fynbos and the dung beetle species (*Bohepilissus nitidus*) restricted to forest, were not clearly negatively impacted by Argentine ant invasion.

The impacts of Argentine ants on non-ant alien invertebrates also differed among species and across habitats, with more positive than negative impacts observed in forest and pine plantation, and only positive impacts recorded in fynbos (Table 4.8). The associations of the three widespread, abundant alien slug species (*Arion hortensis* aggregate, *Deroceras panormitanum* and *Lehmannia valentiana*) with Argentine ants were mostly positive in forest, all positive in fynbos, but all negative in pine plantation. For alien snails, the impacts of Argentine ants were mostly positive. Portuguese millipedes (*Ommatoiulus moreleti*) were negatively associated with Argentine ant presence in forest and pine plantation, but positively in fynbos. Rough woodlice (*Porcellio scaber*) and European wasps (*Vespula germanica*) were positively associated with Argentine ant presence across habitats. Springtails were either absent, not associated or positively associated with Argentine ant presence across habitats.

**Table 4.6.** Impacts of invasion by Argentine ants on the mean  $\pm$  SD abundance of other invertebrate taxa. Impacts were scored as “positive” if there was an increase in mean abundance with invasion, “negative” if there was a decrease in mean abundance with invasion, and “0” if a species was not collected at any site in that habitat. n = number of sites. % = percentage change in abundance with invasion. \* = absent in uninvaded.

Common name	Forest				Fynbos				Pine plantation			
	Absent (n = 3)	Present (n = 5)	Impact	%	Absent (n = 1)	Present (n = 7)	Impact	%	Absent (n = 3)	Present (n = 4)	Impact	%
Bees	0	0	0		0	0.7 $\pm$ 1.1	positive	*	0	0	0	
Beetles	138.3 $\pm$ 55.3	197.2 $\pm$ 59.0	positive	42.55	32	163.1 $\pm$ 292.1	positive	409.82	270.0 $\pm$ 200.2	102.8 $\pm$ 35.4	negative	-61.94
Bristletails	3.7 $\pm$ 1.2	31.2 $\pm$ 50.9	positive	750.91	4	2.6 $\pm$ 4.8	negative	-35.71	1.7 $\pm$ 2.1	0.5 $\pm$ 0.6	negative	-70.00
Bugs	68.0 $\pm$ 17.1	50.0 $\pm$ 28.1	negative	-26.47	10	16.1 $\pm$ 7.1	positive	61.43	97.0 $\pm$ 52.7	138.0 $\pm$ 149.0	positive	42.27
Centipedes	14.3 $\pm$ 8.5	18.2 $\pm$ 11.9	positive	26.98	12	4.0 $\pm$ 4.2	negative	-66.67	14.7 $\pm$ 14.7	7.5 $\pm$ 4.8	negative	-48.86
Cockroaches	24.7 $\pm$ 34.1	9.6 $\pm$ 5.5	negative	-61.08	43	50.6 $\pm$ 30.9	positive	17.61	1.0 $\pm$ 1.0	5.3 $\pm$ 3.9	positive	425.00
Crickets	18.0 $\pm$ 14.1	20.0 $\pm$ 25.0	positive	11.11	17	73.6 $\pm$ 67.7	positive	332.77	45.0 $\pm$ 70.2	38.8 $\pm$ 38.9	negative	-13.89
Earthworms	115.7 $\pm$ 85.5	153.2 $\pm$ 110.5	positive	32.45	5	10.0 $\pm$ 9.8	positive	100.00	20.3 $\pm$ 9.5	50.5 $\pm$ 84.1	positive	148.36
Earwigs	11.3 $\pm$ 13.1	20.2 $\pm$ 17.3	positive	78.24	2	0.4 $\pm$ 1.1	negative	-78.57	16.3 $\pm$ 0.6	3.8 $\pm$ 3.1	negative	-77.04
Flatworms	0	0	0		0	0.6 $\pm$ 1.1	positive	*	0	0	0	
Flies	10.7 $\pm$ 15.0	0.4 $\pm$ 0.9	negative	-96.25	2	0.4 $\pm$ 0.8	negative	-78.57	4.3 $\pm$ 3.8	2.3 $\pm$ 2.2	negative	-48.08
Harvestmen	79.3 $\pm$ 43.0	95.2 $\pm$ 54.7	positive	20.00	19	87.3 $\pm$ 102.6	positive	359.40	155.7 $\pm$ 116.6	47.8 $\pm$ 16.6	negative	-69.33
Lacewings	89.7 $\pm$ 49.2	108.4 $\pm$ 68.8	positive	20.89	16	4.9 $\pm$ 5.2	negative	-69.64	27.7 $\pm$ 10.1	4.5 $\pm$ 2.4	negative	-83.73
Landhoppers	0	0	0		0	0	0		0	0.3 $\pm$ 0.5	positive	*
Millipedes	232.0 $\pm$ 230.1	184.6 $\pm$ 168.3	negative	-20.43	3	23.6 $\pm$ 31.1	positive	685.71	44.7 $\pm$ 33.7	25.3 $\pm$ 10.2	negative	-43.47
Mites	119.3 $\pm$ 60.6	98.8 $\pm$ 65.3	negative	-17.21	10	22.7 $\pm$ 27.0	positive	127.14	102.3 $\pm$ 46.8	85.5 $\pm$ 69.0	negative	-16.45
Moths	60.0 $\pm$ 13.1	35.8 $\pm$ 15.2	negative	-40.33	61	26.9 $\pm$ 29.4	negative	-55.97	74.7 $\pm$ 43.8	37.5 $\pm$ 12.9	negative	-49.78
Praying mantids	13.0 $\pm$ 9.0	22.4 $\pm$ 13.0	positive	72.31	5	1.3 $\pm$ 2.1	negative	-74.29	1.3 $\pm$ 2.3	1.0 $\pm$ 1.4	negative	-25.00

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Pseudoscorpions	0	0.2 ± 0.4	positive	*	0	0.6 ± 0.8	positive	*	0	0.3 ± 0.5	positive	*
Psocids/barklice	2.7 ± 2.1	4.0 ± 4.2	positive	50.00	0	2.0 ± 2.9	positive	*	1.7 ± 1.5	0.8 ± 1.5	negative	-55.00
Scorpions	3.7 ± 2.1	7.2 ± 3.1	positive	96.36	3	2.1 ± 3.1	negative	-28.57	6.3 ± 5.7	9.0 ± 5.2	positive	42.11
Silverfish	2.3 ± 1.5	0.4 ± 0.9	negative	-82.86	0	3.1 ± 2.1	positive	*	1.3 ± 2.3	0.8 ± 1.0	negative	-43.75
Slugs	23.0 ± 7.0	19.4 ± 9.6	negative	-15.65	1	5.1 ± 4.4	positive	414.29	43.0 ± 33.8	7.0 ± 6.8	negative	-83.72
Snails	22.0 ± 14.0	92.2 ± 45.3	positive	319.09	0	7.7 ± 7.6	positive	*	7.7 ± 0.6	17.0 ± 19.9	positive	121.74
Spiders	25.7 ± 5.0	27.6 ± 8.1	positive	7.53	23	36.7 ± 10.9	positive	59.63	17.0 ± 7.8	21.8 ± 11.7	positive	27.94
Springtails	107.0 ± 131.4	241.4 ± 395.3	positive	125.61	11	15.7 ± 7.6	positive	42.86	84.7 ± 81.0	47.5 ± 38.8	negative	-43.90
Stick insects	0	0	0		0	1.9 ± 3.7	positive	*	0.3 ± 0.6	0	negative	-100.00
Sun-spiders	0	0	0		0	1.0 ± 1.8	positive	*	0	0	0	
Thrips	0.3 ± 0.6	0.2 ± 0.4	negative	-40.00	0	0	0		0	0	0	
Velvet worms	1.3 ± 1.5	0.4 ± 0.9	negative	-70.00	0	0	0		0	0.5 ± 1.0	positive	*
Wasps	53.3 ± 51.0	44.0 ± 29.4	negative	-17.50	6	11.3 ± 8.0	positive	88.10	39.0 ± 18.1	38.0 ± 48.8	negative	-2.56
Woodlice	12.3 ± 4.9	29.2 ± 32.8	positive	136.76	2	23.9 ± 52.7	positive	1092.86	0.3 ± 0.6	15.0 ± 25.4	positive	4400.00

**Table 4.7.** Impacts of invasion by Argentine ants on the mean  $\pm$  SD abundance of Cape Peninsula endemic species. Impacts were scored as “positive” if there was an increase in mean abundance with invasion, “negative” if there was a decrease in mean abundance with invasion, “neutral” if there was no difference in mean abundance with invasion, and “0” if a species was not collected at any site in that habitat. n = number of sites. % = percentage change in abundance with invasion. \* = absent in uninvasioned.

Endemic species	Forest				Fynbos				Pine plantation			
	Absent (n = 3)	Present (n = 5)	Impact	%	Absent (n = 1)	Present (n = 7)	Impact	%	Absent (n = 3)	Present (n = 4)	Impact	%
<i>Trachycystis perplicata</i>	0.3 $\pm$ 0.6	1.0 $\pm$ 1.7	positive	200.00	0	0	0		0	0	0	
<i>Spermophora gordimerae</i>	0	1.2 $\pm$ 2.2	positive	*	0	0.4 $\pm$ 0.8	positive	*	0	0	0	
<i>Spermophora peninsulae</i>	0	0.2 $\pm$ 0.4	positive	*	0	0	0		0	0	0	
<i>Malaika longipes</i>	1.0 $\pm$ 1.0	2.2 $\pm$ 1.8	positive	120.00	2	0	negative	-100.00	0	0	0	
<i>Moggridgea teresae</i>	1.0 $\pm$ 1.0	1.0 $\pm$ 1.2	neutral	0.00	0	0.1 $\pm$ 0.4	positive	*	0	0	0	
<i>Uroplectes insignis</i>	2.3 $\pm$ 1.5	0.4 $\pm$ 0.9	positive	-82.86	0	1.9 $\pm$ 2.5	positive	*	1.3 $\pm$ 2.3	0.5 $\pm$ 1.0	negative	-62.50
<i>Dipteretrum brinckae</i>	0	0	0		7	6.6 $\pm$ 14.0	negative	-6.12	0	0	0	
<i>Hoplophoropyga unicolor</i>	0	0	0		0	4.6 $\pm$ 5.4	positive	*	0	0	0	
<i>Bohepilissus nitidus</i>	4.7 $\pm$ 4.5	20.2 $\pm$ 33.0	positive	332.86	0	0	0		0	0	0	

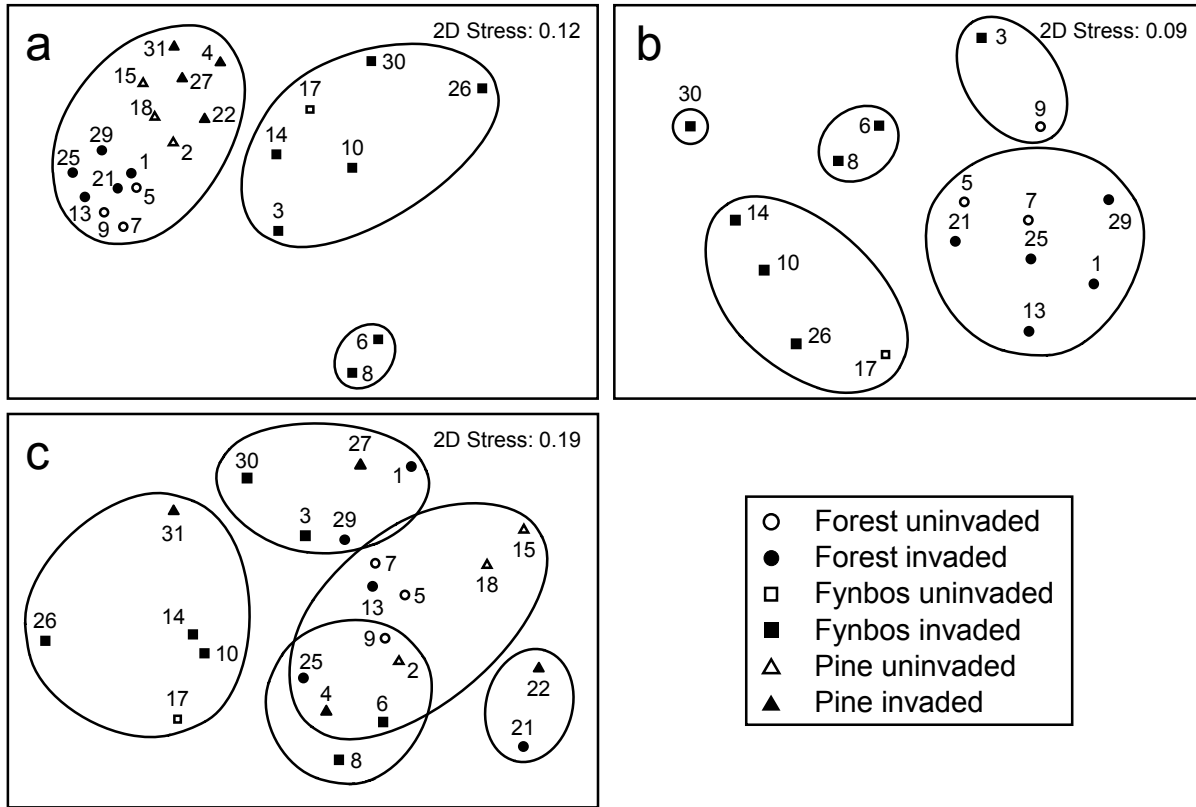
**Table 4.8.** Impacts of invasion by Argentine ants on the mean  $\pm$  SD abundance of other alien species. Impacts were scored as “positive” if there was an increase in mean abundance with invasion, “negative” if there was a decrease in mean abundance with invasion, “neutral” if there was no difference in mean abundance with invasion, and “0” if a species was not collected at any site in that habitat. n = number of sites. % = percentage change in abundance with invasion. \* = absent in uninvaded.

Alien species	Forest				Fynbos				Pine plantation			
	Absent (n = 3)	Present (n = 5)	Impact	%	Absent (n = 1)	Present (n = 7)	Impact	%	Absent (n = 3)	Present (n = 4)	Impact	%
<i>Arion hortensis</i> complex	11.7 $\pm$ 8.3	14.2 $\pm$ 8.8	positive	21.71	1	4.0 $\pm$ 3.8	positive	300.00	30.5	7.0 $\pm$ 6.8	negative	-79.61
<i>Deroceras panormitanum</i>	6.3 $\pm$ 9.2	2.2 $\pm$ 1.8	negative	-65.26	0	0.6 $\pm$ 1.1	positive	*	1.0 $\pm$ 1.7	0	negative	-100.00
<i>Lehmannia valentiana</i>	5.0 $\pm$ 3.6	2.6 $\pm$ 2.6	negative	-48.00	0	0.6 $\pm$ 1.5	positive	*	7.7 $\pm$ 7.1	0	negative	-100.00
<i>Limax maximus</i>	0	0.4 $\pm$ 0.9	positive	*	0	0	0		0	0	0	
<i>Cochlicopa</i> sp.	0	3.2 $\pm$ 7.2	positive	*	0	0	0		0	0	0	
<i>Cochlicopa</i> cf. <i>lubricella</i>	0	11.2 $\pm$ 25.0	positive	*	0	0	0		0	0.8 $\pm$ 1.0	positive	*
<i>Vitrea contracta</i>	2.7 $\pm$ 4.6	1.0 $\pm$ 2.2	negative	-62.50	0	0	0		0.7 $\pm$ 1.2	4.3 $\pm$ 7.2	positive	537.50
<i>Cornu aspersum</i>	0.3 $\pm$ 0.6	1.0 $\pm$ 1.7	positive	200.00	0	0	0		0	0	0	
cf. <i>Punctum</i> sp.	0	7.0 $\pm$ 15.7	positive	*	0	0	0		5.7 $\pm$ 3.2	5.3 $\pm$ 7.4	negative	-7.35
<i>Lauria cylindracea</i>	0	0	0		0	0	0		0	0.3 $\pm$ 0.5	positive	*
<i>Oxychilus draparnaudi</i>	0	12.0 $\pm$ 24.0	positive	*	0	0.3 $\pm$ 0.8	positive	*	0	3.3 $\pm$ 6.5	positive	*
<i>Oxychilus</i> sp.	0	1.8 $\pm$ 3.0	positive	*	0	1.4 $\pm$ 3.4	positive	*	0	2.5 $\pm$ 4.4	positive	*
<i>Ommatoiulus moreletii</i>	83.7 $\pm$ 33.3	51.4 $\pm$ 34.0	negative	-38.57	10	20.3 $\pm$ 27.3	positive		87.3 $\pm$ 33.0	71.0 $\pm$ 51.0	negative	-18.70
<i>Porcellio scaber</i>	2.0 $\pm$ 1.0	8.6 $\pm$ 13.7	positive	330.00	0	14.1 $\pm$ 28.9	positive	*	0.3 $\pm$ 0.6	1.8 $\pm$ 2.0	positive	425.00
<i>Entomobrya nivalis</i>	0	0	0		0	0	0	102.86	5.3 $\pm$ 9.2	0	negative	-100.00
<i>Neanura muscorum</i>	0	0.2 $\pm$ 0.4	positive	*	0	0.6 $\pm$ 1.5	positive	*	0.3 $\pm$ 0.6	0.3 $\pm$ 0.5	neutral	-25.00
<i>Tomocerus minor</i>	0	0	0		0	0.1 $\pm$ 0.4	positive	*	0	0	0	
<i>Vesputula germanica</i>	1.3 $\pm$ 2.3	2.2 $\pm$ 4.4	positive	65.00	0	2.0 $\pm$ 3.5	positive	*	0.3 $\pm$ 0.6	0.5 $\pm$ 1.0	positive	50.00

The community composition of all other non-ant invertebrates differed between habitats, with sites clustering according to habitat, irrespective of Argentine ant presence-absence (Fig. 4.7a). All forest and pine plantation sites clustered together, separately from fynbos sites, with only 30.7% similarity among habitat clusters. Pine plantation and forest sites could be further separated with 35.1% similarity between them (not shown on MDS plot). Although there appears to be some separation of uninvaded and invaded sites in pine plantation and forest, this was not supported by the dendrogram clustering pattern. Sites 6 and 8, the two Granite Fynbos sites, clustered separately from all other sites. Recovering Sandstone Fynbos (Sites 3 and 30) clustered amongst the other Sandstone Fynbos sites, and not with pine plantation sites.

The community composition of Cape Peninsula endemic invertebrates differed between forest and fynbos, and among fynbos types, but was not determined by Argentine ant presence-absence (Fig. 4.7b). Sites clustered broadly into forest and fynbos, with 29.6% similarity between these two groups (not shown on MDS). Sites could be further divided based on their vegetation type and disturbance history, with 44.9% similarity among clusters (grouping shown in Fig. 4.7b). Granite Fynbos (Sites 6 and 8) clustered separately from Sandstone Fynbos (Sites 10, 14, 17 and 26) and recovering fynbos (Sites 3 and 30).

The community composition of non-ant alien invertebrates was not clearly determined by either habitat or Argentine ant presence-absence (Fig. 4.7c). At 41.5% similarity between clusters (grouping shown in Fig. 4.7c), site clusters overlapped and no meaningful grouping was detected in the dendrogram. The stress value was high (0.19), implying that these patterns may not be reliable, with a risk of drawing false inferences if followed.



**Figure 4.7.** MDS ordination applied to Bray-Curtis dissimilarity matrices of fourth-root transformed data of community composition amongst sites where Argentine ants were present (invaded) and absent (uninvaded) for (a) all non-ant invertebrates, (b) Cape Peninsula endemic invertebrates and (c) non-ant alien invertebrates. For Cape Peninsula endemic invertebrates, pine plantation sites were excluded because endemics were mostly absent in pine plantation.

Pairwise ANOSIM test results, such as pine invaded versus forest unin invaded, that had no direct relevance to the null hypothesis, were omitted from all analyses of Argentine ant invasion impacts on the community composition of non-ant invertebrates. ANOSIM for all non-ant invertebrates confirmed that habitat (vegetation type) had a stronger influence on community composition than Argentine ant presence-absence (Table 4.9). No significant difference in community composition of non-ant invertebrates between sites unin invaded and invaded by Argentine ants was found within forest, fynbos or pine plantation. However, there were significant differences between pairwise combinations of habitats for invaded sites: forest invaded vs. fynbos invaded ( $R = 0.672$ ,  $p = 0.003$ ), and forest invaded vs. pine invaded ( $R = 0.867$ ,  $p = 0.018$ ) (Table 4.9). These results confirm the pattern observed in the MDS ordination (Fig. 4.7a) of sites being separated by habitat and not by Argentine ant presence-absence.



Similarly, ANOSIM for Cape Peninsula endemic invertebrate species showed that the community composition of sites where Argentine ants were present differed significantly between forest and fynbos ( $R = 0.740$ ,  $p = 0.001$ ) (Table 4.9). Argentine ant invasion did not significantly alter the community composition of endemic species within habitats. These results confirm the pattern observed in the MDS ordination (Fig. 4.7b) of sites separated by habitat and not by Argentine ant presence-absence.

ANOSIM for other alien invertebrates showed no difference in community composition between sites where Argentine ants were present and absent, either within or between habitats (Table 4.9). This explained the lack of detectable pattern in the MDS ordination (Fig. 4.7c), in which clusters overlapped and were not clearly defined either by habitat or Argentine ant presence-absence.

**Table 4.9.** ANOSIM results for the community composition of all other non-ant, Cape Peninsula endemic, and non-ant alien invertebrates at sites where Argentine ants were present (invaded) and absent (uninvaded). Values in bold are significant ( $p < 0.05$ ).

Habitat pairs	All non-ants		Endemics		Aliens	
	<i>R</i>	<i>p</i>	<i>R</i>	<i>p</i>	<i>R</i>	<i>p</i>
Forest invaded vs. Forest uninvaded	-0.200	0.857	-0.056	0.589	-0.251	0.982
Fynbos invaded vs. Fynbos uninvaded	-0.102	0.750	0.252	0.250	-0.034	0.750
Pine invaded vs. Pine uninvaded	0.037	0.571	*		-0.204	0.857
Forest invaded vs. Fynbos invaded	<b>0.672</b>	<b>0.003</b>	<b>0.740</b>	<b>0.001</b>	0.209	0.085
Forest invaded vs. Pine invaded	<b>0.867</b>	<b>0.018</b>	*		0.119	0.254
Fynbos invaded vs. Pine invaded	<b>0.328</b>	<b>0.048</b>	*		0.212	0.094
Forest uninvaded vs. Fynbos uninvaded	1.000	0.250	0.556	0.500	1.000	0.250
Forest uninvaded vs. Pine uninvaded	0.963	0.100	*		0.370	0.200
Fynbos uninvaded vs. Pine uninvaded	1.000	0.250	*		1.000	0.250

\*Comparisons with pine omitted, because endemic species were mostly absent in pine plantation.

### *Other alien invertebrates*

Eighteen non-ant alien invertebrate species were collected in forest, fynbos and pine plantation. The native invertebrate assemblage, against which the impacts of these alien taxa were compared, consisted of eight mollusc, nine millipede, six woodlice, 16 springtail and 107 wasp species. Across habitats, there was no correlation between the abundance of most alien invertebrate species and either the species richness (Table 4.10) or abundance (Table 4.11) of native species in each alien's corresponding taxon. Significant, positive Spearman rank correlations between alien abundance and equivalent native species richness in all habitats combined were found for *Deroceras panormitanum*, *Ommatoiulus moreleti* and *Neanura muscorum* (Table 4.10). Significant, positive correlations between alien and equivalent native taxa abundances in all habitats combined were found for *D. panormitanum*, *Cornu aspersum*, *O. moreleti* and *Vespula germanica* (Table 4.11). In forest, wasp species richness was significantly positively correlated with *V. germanica* abundance (Table 4.10), and snail abundance was significantly positively correlated with *Vitrea contracta* abundance (Table 4.11). In fynbos, snail species richness was significantly positively correlated with *D. panormitanum* abundance (Table 4.10). In pine plantation, millipede species richness and abundance were significantly positively correlated with *O. moreleti* abundance, and wasp abundance was significantly correlated with *V. germanica* abundance. Both native snail species richness (Table 4.10) and abundance (Table 4.11) were negatively (although not significantly) correlated with the abundance of the carnivorous alien snail *Oxychilus draparnaudi*.

Mean  $\pm$  SD species richness of native invertebrates in the taxon to which each alien belongs was generally higher at sites where the alien species did not occur (Table 4.12). This association of native species with an alien species was only statistically significant for *D. panormitanum* (Mann-Whitney *U* test:  $Z = 3.939$ ,  $p < 0.001$ ) and *N. muscorum* ( $Z = -2.433$ ,  $p = 0.009$ ) across habitats. Mean  $\pm$  SD abundance of taxonomic equivalent native invertebrates was also generally higher at sites where the alien species was absent, but again variable amongst species and habitats (Table 4.13). This association of native abundance with the presence of an alien species was only statistically significant for *D. panormitanum* ( $Z = 3.631$ ,  $p < 0.001$ ), *C. aspersum* ( $Z = 2.100$ ,  $p = 0.026$ ) and *V. germanica* ( $Z = -2.741$ ,  $p = 0.004$ ) across habitats.

**Table 4.10.** Spearman rank correlations between the abundance of each alien invertebrate species collected and the species richness of native species from the corresponding taxon to which the alien belongs. Values in bold are significant ( $p < 0.05$ ).

Alien	Corresponding Taxon	All habitats		Forest		Fynbos		Pine	
		<i>R</i>	<i>p</i>	<i>R</i>	<i>p</i>	<i>R</i>	<i>p</i>	<i>R</i>	<i>p</i>
<i>Arion hortensis</i> aggregate	Snails	0.319	0.137	-0.236	0.573	0.619	0.102	0.316	0.446
<i>Deroceras panormitanum</i>	Snails	<b>0.866</b>	<b>&lt;0.001</b>	0.326	0.431	<b>0.761</b>	<b>0.028</b>	0.667	0.071
<i>Lehmannia valentiana</i>	Snails	0.159	0.470	-0.481	0.227	-0.354	0.390	-0.016	0.970
<i>Limax maximus</i>	Snails	0.050	0.822	-0.514	0.193	*	*	*	*
<i>Cochlicopa</i> sp.	Snails	0.348	0.104	0.514	0.193	*	*	*	*
<i>Cochlicopa</i> cf. <i>lubricella</i>	Snails	0.051	0.816	0.514	0.193	*	*	0.135	0.750
<i>Vitrea contracta</i>	Snails	0.156	0.476	<b>0.776</b>	<b>0.023</b>	*	*	0.206	0.624
<i>Cornu aspersum</i>	Snails	0.332	0.122	-0.221	0.599	*	*	*	*
cf. <i>Punctum</i> sp.	Snails	-0.239	0.271	-0.514	0.193	*	*	0.498	0.209
<i>Lauria cylindracea</i>	Snails	-0.066	0.764	*	*	*	*	0.381	0.352
<i>Oxychilus draparnaudi</i>	Snails	0.023	0.916	-0.226	0.590	-0.354	0.390	-0.432	0.285
<i>Oxychilus</i> sp.	Snails	-0.264	0.224	-0.421	0.299	-0.535	0.172	-0.571	0.139
<i>Ommatoiulus moreleti</i>	Millipedes	<b>0.536</b>	<b>0.008</b>	0.159	0.708	0.201	0.632	<b>0.712</b>	<b>0.048</b>
<i>Porcellio scaber</i>	Woodlice	0.261	0.230	0.085	0.841	0.276	0.508	0.201	0.633
<i>Entomobrya nivalis</i>	Springtails	0.365	0.087	*	*	*	*	0.607	0.111
<i>Neanura muscorum</i>	Springtails	<b>0.545</b>	<b>0.007</b>	0.514	0.193	1	0.105	0.475	0.234
<i>Tomocerus minor</i>	Springtails	0.083	0.707	*	*	0.176	0.677	*	*
<i>Vespa germanica</i>	Wasps	0.388	0.068	0.607	0.110	0.383	0.349	0.201	0.634

\* Alien species not collected in that habitat

**Table 4.11.** Spearman rank correlations between the abundance of each alien invertebrate species collected and the abundance of native species from the corresponding taxon to which the alien belongs. Values in bold are significant ( $p < 0.05$ ).

Alien	Corresponding taxon	All habitats		Forest		Fynbos		Pine	
		<i>R</i>	<i>p</i>	<i>R</i>	<i>p</i>	<i>R</i>	<i>p</i>	<i>R</i>	<i>p</i>
<i>Arion hortensis</i> aggregate	Snails	0.317	0.141	-0.467	0.243	0.484	0.224	0.454	0.259
<i>Deroceras panormitanum</i>	Snails	<b>0.768</b>	<b>&lt;0.001</b>	0.218	0.604	0.697	0.054	0.286	0.493
<i>Lehmannia valentiana</i>	Snails	0.232	0.286	-0.217	0.606	-0.351	0.393	0.142	0.738
<i>Limax maximus</i>	Snails	0.115	0.601	-0.412	0.310	*	*	*	*
<i>Cochlicopa</i> sp.	Snails	0.214	0.327	-0.082	0.846	*	*	*	*
<i>Cochlicopa</i> cf. <i>lubricella</i>	Snails	-0.016	0.944	-0.082	0.846	*	*	0.297	0.475
<i>Vitrea contracta</i>	Snails	0.022	0.919	-0.265	0.526	*	*	0.429	0.289
<i>Cornu aspersum</i>	Snails	<b>0.475</b>	<b>0.022</b>	0.385	0.346	*	*	*	*
cf. <i>Punctum</i> sp.	Snails	-0.302	0.162	-0.412	0.310	*	*	0.498	0.209
<i>Lauria cylindracea</i>	Snails	-0.033	0.882	*	*	*	*	0.571	0.139
<i>Oxychilus draparnaudi</i>	Snails	0.072	0.744	-0.109	0.797	-0.351	0.393	-0.432	0.285
<i>Oxychilus</i> sp.	Snails	-0.156	0.478	0.069	0.872	-0.531	0.175	-0.571	0.139
<i>Ommatoiulus moreleti</i>	Millipedes	<b>0.655</b>	<b>&lt;0.001</b>	0.371	0.365	0.043	0.919	<b>0.826</b>	<b>0.011</b>
<i>Porcellio scaber</i>	Woodlice	0.328	0.127	0.530	0.176	0.416	0.306	0.291	0.485
<i>Entomobrya nivalis</i>	Springtails	0.289	0.180	*	*	*	*	0.577	0.134
<i>Neanura muscorum</i>	Springtails	0.239	0.272	0.577	0.134	0	0.615	0.312	0.452
<i>Tomocerus minor</i>	Springtails	-0.225	0.302	*	*	-0.249	0.552	*	*
<i>Vespa germanica</i>	Wasps	<b>0.554</b>	<b>0.006</b>	<b>0.768</b>	<b>0.026</b>	0.659	0.076	<b>0.764</b>	<b>0.027</b>

\* Alien species not collected in that habitat

**Table 4.12.** Mean native taxon species richness compared between sites where alien species were present and absent in each habitat. Values in parentheses refer to the number of sites.

Alien species	Forest		Fynbos		Pine plantation	
	Mean ± SD (sites)		Mean ± SD (sites)		Mean ± SD (sites)	
	present	absent	present	absent	present	absent
<i>Arion hortensis</i> complex	3.4 ± 1.2 (8)	(0)	1.1 ± 1.2 (7)	0 (1)	0.8 ± 1.2 (6)	0 (1)
<i>Deroceras panormitanum</i>	3.4 ± 1.2 (8)	(0)	2.5 ± 0.7 (2)	0.5 ± 0.8 (6)	3 (1)	0.3 ± 0.5 (6)
<i>Lehmannia valentiana</i>	3.2 ± 1.2 (6)	4.0 ± 1.4 (2)	0 (1)	1.1 ± 1.2 (7)	0.5 ± 0.7 (2)	0.8 ± 1.3 (5)
<i>Limax maximus</i>	2 (1)	3.6 ± 1.1 (7)	(0)	1.0 ± 1.2 (8)	(0)	0.7 ± 1.1 (7)
<i>Cochlicopa</i> sp.	5 (1)	3.1 ± 1.1 (7)	(0)	1.0 ± 1.2 (8)	(0)	0.7 ± 1.1 (7)
<i>Cochlicopa</i> cf. <i>lubricella</i>	5 (1)	3.1 ± 1.1 (7)	(0)	1.0 ± 1.2 (8)	0.5 ± 0.7 (2)	0.8 ± 1.3 (5)
<i>Vitrea contracta</i>	5.0 ± 0 (2)	2.8 ± 0.8 (6)	(0)	1.0 ± 1.2 (8)	0.7 ± 0.6 (3)	0.8 ± 1.5 (4)
<i>Cornu aspersum</i>	3.0 ± 1.0 (3)	3.6 ± 1.3 (5)	(0)	1.0 ± 1.2 (8)	(0)	0.7 ± 1.1 (7)
cf. <i>Punctum</i> sp.	2 (1)	3.6 ± 1.1 (7)	(0)	1.0 ± 1.2 (8)	0.8 ± 1.2 (6)	0 (1)
<i>Lauria cylindracea</i>	(0)	3.4 ± 1.2 (8)	(0)	1.0 ± 1.2 (8)	1 (1)	0.7 ± 1.2 (6)
<i>Oxychilus draparnaudi</i>	3.3 ± 1.5 (3)	1.5 ± 1.1 (5)	0 (1)	1.1 ± 1.2 (7)	0 (1)	0.8 ± 1.2 (6)
<i>Oxychilus</i> sp.	2.7 ± 0.6 (3)	3.8 ± 1.3 (5)	0.0 ± 0.0 (2)	1.3 ± 1.2 (6)	0.0 ± 0.0 (2)	1.0 ± 1.2 (5)
<i>Ommatoiulus moreletii</i>	3.1 ± 1.6 (8)	(0)	1.4 ± 1.4 (8)	(0)	2.9 ± 1.5 (7)	(0)
<i>Porcellio scaber</i>	2.8 ± 1.5 (6)	1.5 ± 2.1 (2)	0.5 ± 0.5 (6)	0.5 ± 0.7 (2)	0.0 ± 0.0 (3)	0.3 ± 0.5 (4)
<i>Entomobrya nivalis</i>	(0)	3.6 ± 1.1 (8)	(0)	3.4 ± 1.3 (8)	9 (1)	3.2 ± 1.3 (6)
<i>Neanura muscorum</i>	5 (1)	3.4 ± 1.0 (7)	4 (1)	3.1 ± 1.2 (7)	6.5 ± 3.5 (2)	3.0 ± 1.4 (5)
<i>Tomocerus minor</i>	(0)	3.6 ± 1.1 (8)	4 (1)	3.3 ± 1.4 (7)	(0)	4.0 ± 2.5 (7)
<i>Vespula germanica</i>	24.0 ± 10.4 (3)	12.6 ± 7.1 (5)	7.0 ± 0.0 (2)	5.0 ± 2.4 (6)	12.5 ± 7.8 (2)	9.0 ± 5.1 (5)

**Table 4.13.** Mean native taxon abundance compared between sites where alien species were present and absent in each habitat.

Values in parentheses refer to the number of sites.

Alien species	Forest		Fynbos		Pine plantation	
	Mean $\pm$ SD (sites)		Mean $\pm$ SD (sites)		Mean $\pm$ SD (sites)	
	Present	absent	present	absent	present	absent
<i>Arion hortensis</i> complex	41.5 $\pm$ 48.0 (8)	(0)	6.0 $\pm$ 8.4 (7)	0 (1)	1.2 $\pm$ 1.5 (6)	0 (1)
<i>Deroceras panormitanum</i>	41.5 $\pm$ 48.0 (8)	(0)	14.5 $\pm$ 4.0 (2)	2.2 $\pm$ 12.0 (6)	3 (1)	1.0 $\pm$ 1.5 (6)
<i>Lehmannia valentiana</i>	41.5 $\pm$ 55.5 (6)	41.5 $\pm$ 26.2 (2)	0 (1)	6.0 $\pm$ 8.4 (7)	1.5 $\pm$ 2.1 (2)	0.8 $\pm$ 1.3 (5)
<i>Limax maximus</i>	10 (1)	46.0 $\pm$ 49.9 (7)	(0)	5.3 $\pm$ 8.0 (8)	(0)	0.7 $\pm$ 1.4 (7)
<i>Cochlicopa</i> sp.	23 (1)	44.1 $\pm$ 51.2 (7)	(0)	5.3 $\pm$ 8.0 (8)	(0)	0.7 $\pm$ 1.4 (7)
<i>Cochlicopa</i> cf. <i>lubricella</i>	23 (1)	44.1 $\pm$ 51.2 (7)	(0)	5.3 $\pm$ 8.0 (8)	1.5 $\pm$ 2.1 (2)	0.8 $\pm$ 1.3 (5)
<i>Vitrea contracta</i>	21.5 $\pm$ 2.1 (2)	48.2 $\pm$ 54.8 (6)	(0)	5.3 $\pm$ 8.0 (8)	2.0 $\pm$ 1.7 (3)	0.3 $\pm$ 0.5 (4)
<i>Cornu aspersum</i>	64.7 $\pm$ 77.2 (3)	27.6 $\pm$ 20.0 (5)	(0)	5.3 $\pm$ 8.0 (8)	(0)	0.7 $\pm$ 1.4 (7)
cf. <i>Punctum</i> sp.	10 (1)	46.0 $\pm$ 49.9 (7)	(0)	5.3 $\pm$ 8.0 (8)	1.2 $\pm$ 1.5(6)	0 (1)
<i>Lauria cylindracea</i>	(0)	41.5 $\pm$ 48.0 (8)	(0)	5.3 $\pm$ 8.0 (8)	3 (1)	0.7 $\pm$ 1.2 (6)
<i>Oxychilus draparnaudi</i>	31.0 $\pm$ 25.9 (3)	47.8 $\pm$ 59.6 (5)	0 (1)	6.0 $\pm$ 8.4 (7)	0 (1)	1.2 $\pm$ 1.5 (6)
<i>Oxychilus</i> sp.	33.0 $\pm$ 25.2 (3)	46.6 $\pm$ 60.2 (5)	0.0 $\pm$ 0.0 (2)	7.0 $\pm$ 8.7 (6)	0.0 $\pm$ 0.0 (2)	1.4 $\pm$ 1.5 (5)
<i>Ommatoiulus moreletii</i>	43.0 $\pm$ 45.2 (8)	(0)	2.1 $\pm$ 2.5 (8)	(0)	14.7 $\pm$ 16.0 (7)	(0)
<i>Porcellio scaber</i>	21.5 $\pm$ 19.3 (6)	2.5 $\pm$ 3.5 (2)	11.3 $\pm$ 25.8 (6)	1.0 $\pm$ 1.4 (2)	0.0 $\pm$ 0.0 (3)	13.3 $\pm$ 26.5 (4)
<i>Entomobrya nivalis</i>	(0)	190.9 $\pm$ 314.4 (8)	(0)	14.5 $\pm$ 7.3 (8)	148 (1)	46.3 $\pm$ 40.0 (6)
<i>Neanura muscorum</i>	945 (1)	15.6 $\pm$ 83.6 (7)	13 (1)	15.9 $\pm$ 7.8 (7)	93.5 $\pm$ 77.1 (2)	20.0 $\pm$ 44.5 (5)
<i>Tomocerus minor</i>	(0)	190.9 $\pm$ 314.4 (8)	12 (1)	14.9 $\pm$ 7.8 (7)	(0)	60.9 $\pm$ 53.0 (7)
<i>Vespula germanica</i>	76.0 $\pm$ 27.6 (3)	27.4 $\pm$ 20.9 (5)	14.5 $\pm$ 4.9 (2)	7.0 $\pm$ 3.3 (6)	83.0 $\pm$ 36.8 (2)	20.0 $\pm$ 10.8 (5)

The community composition of native snails, millipedes, woodlice, springtails and wasps was not structured according to the presence-absence of corresponding alien species. In MDS ordinations, sites did not cluster according to alien presence-absence, or a combination of alien presence-absence with habitat, so were not presented. ANOSIM showed that native snail community composition was not significantly different between sites where *D. panormitanum* was present and absent in each habitat. There was also no significant difference in snail community composition based on the presence-absence of the other alien molluscs. Springtail community composition compared between the presence and absence of *N. muscorum* was significantly different ( $R = 0.727$ ,  $p = 0.048$ ) in pine plantation, but not in forest or fynbos. *P. scaber* and *V. germanica* showed no significant influence on woodlice and wasp community composition respectively.

## Discussion

### *Argentine ants and native ants*

The lack of apparent difference in sites invaded by Argentine ants, compared to sites where Argentine ants were absent, is a surprising result. Luruli (2007) found that in fynbos, native ant species richness may be eight times lower at Argentine ant invaded, compared to uninvaded, bait stations. Reduced native ant species richness and abundance in the presence of Argentine ants has also been reported in California (Heller *et al.*, 2008), Spain (Oliveras *et al.*, 2005), Australia (Walters, 2006) and Japan (Touyama *et al.*, 2003). In this study, no clear evidence was found for negative Argentine ant impacts on the mean species richness (Fig. 4.2a), mean abundance (Fig. 4.2b and Table 4.2), or community composition (Fig. 4.4 and Table 4.3) of native ant species in forest, fynbos or pine plantation on the Cape Peninsula.

Although Argentine ants were present at 16 of the 23 sites sampled, they were not collected in high abundance at all of these sites. Ant nests, including those belonging to Argentine ants, were not specifically searched for in this study. The sites sampled in this study were patch-mosaic in nature and in relatively close proximity to one another (different habitats were often adjoining), with strong edge effects likely for many of these small, remnant patches of native vegetation. Consequently, it remains unclear whether Argentine ants are able to establish permanent colonies in undisturbed fynbos on the Cape Peninsula, as has been reported in other protected areas (e.g. Kogelberg Biosphere Reserve: Christian, 2001).

Native ant assemblages in forest appear to be similar to those in the adjacent exotic pine plantation, irrespective of Argentine ant presence/absence. This was expected, since most ant

species in pine plantation probably originated from native forest and/or represent widespread, habitat-generalist species. Of the six species not collected in pine plantation, *Myrmicaria nigra* and *Pheidole capensis* are seed-harvesters (Table 4.2). These species may not naturally survive under pine. Cape Peninsula pine plantations support few flowering plants and hardly ever any Proteaceae, so offer few opportunities for seed-harvesting ants.

Nonetheless, the most parsimonious explanation for this apparent lack of impact of Argentine ants on native ants can be ascribed to the disturbance history of these sites. Argentine ant invasion varies with habitat structure, especially with past disturbance history. This covarying habitat structure may also be causing the variation in native ant assemblage composition and not Argentine ants themselves, or at least not alone. Only long-term experimental manipulations may clearly resolve such confounding causative variables.

Invasive ant species are known to reduce native species richness, rapidly disassemble native ant communities, and alter community organisation amongst the species that persist (Sanders *et al.*, 2003). This disrupted ant community pattern in the presence of invasive ants is evident at both biogeographic and local scales. In a local-scale study in fynbos, Luruli (2007) found altered ant community patterns with invasion: native ants were negatively associated (suggesting segregation) at uninvaded bait stations, but significantly positively associated (suggesting aggregation) at bait stations invaded by Argentine ants.

In this study there was evidence for nonrandom co-occurrence of native ant species, suggesting an aggregated community, in fynbos and pine plantations sites where Argentine ants were present (Table 4.4). However, without being able to show significant changes in co-occurrence patterns with alien invasion (*i.e.* between sites where Argentine ants were present and absent), it cannot be confidently concluded that Argentine ants are responsible for ant community disassembly on the Cape Peninsula. Fynbos is a naturally heterogeneous habitat, so nonrandom, aggregated spatial distributions are to be expected (Hui *et al.*, 2010), even in the absence of a dominant invasive ant species.

In forest sites in this study there was no evidence for nonrandom co-occurrence patterns of native ants, suggesting that Argentine ants do not influence community composition (Table 4.4). However, in assuming that all sites are equiprobable (because they are of similar size and quality), negative co-occurrence patterns may be hidden by heterogeneity among sites (Gotelli & McCabe, 2002). Afrotropical forest, like fynbos on the Cape Peninsula, is naturally heterogeneous. C-score may also be overly conservative, because it does not take differences in abundance into account.



The functional group approach was originally designed in Australia (Andersen, 1997a; Hoffmann & Andersen, 2003; Majer *et al.*, 2004). It has useful applications in other regions (Andersen, 1997a), and is relevant in South Africa, because many of the common Australian ant genera also occur here (Andersen & Majer, 2004). Nevertheless, the functional group scheme has limitations for studies of community dynamics at local scales, when a detailed understanding of the impacts on individual species is needed (Andersen, 2010). Firstly, functional groups based on niche dimensions tend to be purely descriptive, even though they are based on global-scale responses of ants to environmental stress and disturbance at the genus or species-group level (Andersen, 2010). Secondly, functional group comparisons are limited, because they were designed for continental and intercontinental analyses of biogeographic patterns of community structure, and responses to disturbance (Andersen, 1997a; Hoffmann & Andersen, 2003). Therefore, functional group comparisons may not always offer reliable interpretation at local scales.

Despite these limitations, the functional group approach shows potential for explaining the impacts of invasive ants. In South Australia, sites invaded by Argentine ants supported greater proportions of Generalized Myrmicinae, Cold Climate Specialists, and Specialised Predators (Walters, 2006). In this study, the native ant community was represented by six functional groups (Table 4.5), which in most instances had lower mean abundance in the presence of Argentine ants (Fig. 4b).

Generalized Myrmicinae and Subordinate Camponotini species richness was unaffected by invasion, suggesting that they can co-occur, even though their numbers were lower. Nevertheless, impacts may differ at the species level and in different habitats. Specialist Predators had fewer individuals at invaded sites in fynbos, suggesting they may be unable to coexist with Argentine ants. Climate Specialists, such as *Meranoplus* (HCS) and *Tetraponera* (TCS), generally occur in habitats where native Dominant Dolichoderinae are not dominant or abundant (Andersen, 1997a; Holway, 1999; Andersen, 2000), contrary to the findings here. However, this may simply reflect a limitation of the genus-level based functional group approach. Luruli (2007) did not collect *Tetraponera*, so comparisons in other fynbos regions are not yet possible. Opportunists had consistently more species and a higher mean number of individuals in the presence of Argentine ants in each habitat. This functional group was the most taxonomically diverse (three subfamilies, four genera and five species) of those represented (Table 4.5).

This study, like that of Gotelli & Arnett (2000) and many others, is only a snapshot comparison of invaded and uninvaded sites, and suffers from at least two potential

shortcomings (Sanders *et al.*, 2003). Firstly, invaded and uninvaded sites may vary in ways that either promote invasive species or disadvantage native species. For example, differing disturbance levels apply to the fynbos sites in this study. Two of the invaded sites where Argentine ants were abundant were recovering Sandstone Fynbos (Sites 3 and 30). These sites were previously under pine plantation, and this historic disturbance may have facilitated invasion, or acted in concert with Argentine ant invasion to influence community composition. Secondly, snapshot studies cannot determine whether invaded sites differed from uninvaded sites in species richness and community composition patterns prior to invasion. If not acknowledged, these shortcomings could lead to misinterpretation of the impacts of invasive alien species on community organisation. It is not known how many of the “uninvaded” sites sampled here were previously invaded by Argentine ants. There is some evidence for a dynamic invasion front, since Argentine ants were previously collected at Site 2 (pine) by Raharinjanahary (2007), but were not found there two years later. The impacts of invasion may have a long-lasting effect on the community, even after Argentine ants have abandoned a site.

#### *Argentine ants and other invertebrates*

Non-ant invertebrates are affected by both the direct impacts of invasive alien ants and the resultant indirect impacts of the displacement of native ants (Holway *et al.*, 2002). Displacement of other invertebrates often leads to cascading effects on ecosystems, and disrupts ecosystem processes (Human & Gordon, 1997). However, clear impacts of invasive ants on entire invertebrate communities have seldom been reported, and were not found in this study.

Neither non-ant invertebrate species richness (Fig. 4.6a), nor community composition (Fig. 4.7a), showed an impact of Argentine ant invasion. A previous study in fynbos on the Cape Peninsula also showed that Argentine ants had little impact on ground-dwelling invertebrate diversity (Pryke & Samways, 2010). Weak community-level effects of Argentine ants on ground-dwelling arthropods have been reported in riparian woodlands in northern California (Holway, 1998) and urban parklands in Adelaide, Australia (Walters, 2006). In all these habitats, the impacts of invasive ants may be difficult to detect, because communities were most likely shaped by native ant predation prior to invasion (Cole *et al.*, 1992). The most severe impacts of invasive ants on invertebrate communities are often seen soon after invasion (Heller *et al.*, 2008), whereas Argentine ants have been established on the Cape Peninsula for about a century (Skaife, 1961; 1962; Richardson *et al.*, 1992).

Community-level impacts of Argentine ant invasion were not clear in this study, because the impacts on the mean abundance of individual non-ant invertebrate taxa (mostly orders)

differed among taxa (Table 4.6). Investigations of impacts at the ordinal level may be too coarse, since behavioural and life history traits vary widely within several orders. Beetles are a prime example. Predatory beetles, such as Carabidae, may be severely negatively affected by Argentine ant invasion (Cole *et al.*, 1992), either because they compete with Argentine ants for arthropod prey, or have vulnerable soil-inhabiting larvae. Boring beetles, such as Scolytidae, for example, should be less vulnerable to attack. Argentine ants do not appear to have an obvious negative impact on xylophagous or xylomycophagous communities in forest or pine plantation on the Cape Peninsula (Raharinjanahary, 2007). Body size may also influence the impacts of invasive ants on invertebrates, with effects intuitively expected to be more pronounced in small species.

Furthermore, the data collected here do not provide any evidence for a synergistic impact of pine plantations acting in concert with Argentine ants (Fig. 4.7a). It is not yet clear whether, or how, Argentine ants interact with plantations or invasive stands of alien woody plants to impact native invertebrate species richness, abundance or community composition.

For Cape Peninsula endemic invertebrates, mean species richness (Fig. 4.6c) and abundance (Fig. 4.6d) were slightly (but not significantly) higher at sites where Argentine ants were present. Since populations of endemic invertebrates often occur naturally in low densities, the impacts of Argentine ants are usually difficult to demonstrate statistically, as was the case for endemic arthropods on Hawaii (Cole *et al.*, 1992). This may also apply to several endemic species collected in low numbers in this study. Cole *et al.* (1992) did show negative impacts of Argentine ants on ground-dwelling, endemic, flightless beetles. While the abundance of *Bohepilissus nitidus*, a tiny Cape Peninsula endemic dung beetle, was positively associated with Argentine ant presence in Afrotropical forest (Table 4.7), confounding (unmeasurable) variables and the low number of replicated sites needs to be considered. Contrary to prediction, the community composition of Cape Peninsula endemic species was not apparently influenced by Argentine ant presence-absence, either within, or between, forest and fynbos (Fig. 4.7b and Table 4.9).

For non-ant alien invertebrates, mean species richness (Fig. 4.6e) and abundance (Fig. 4.6f) were slightly (although not statistically significantly) higher at sites where Argentine ants were present in forest and fynbos, but not in pine plantation. Most non-ant alien invertebrate species showed positive associations with invasion by Argentine ants across habitats (Table 4.8), but these impacts varied among taxa. This may suggest a common invasion susceptibility and/or disturbance history of certain sites, for various reasons, rather than an effect of Argentine

ants. The community composition of non-ant alien invertebrates (Fig. 4.7c and Table 4.9) was again not primarily determined by Argentine ant presence-absence.

#### *Other alien invertebrates*

The ecological impacts of most alien invertebrates have not been studied in South Africa. This applies to alien molluscs, despite several species showing negative economic impacts as crop pests (Herbert, 2010). Among the alien molluscs recorded in this study, *Oxychilus draparnaudi*, *Arion hortensis*, *Deroceras panormitanum* and *Limax maximus* have also invaded native forest in New Zealand (Mahlfeld, 2000), where their ecological impacts have been studied. In the Waipipi Scenic Reserve in New Zealand, native snail species richness and abundance have decreased substantially since the carnivorous *A. hortensis* and *Cochlicopa lubrica* were first reported in 1981 (Mahlfeld, 2000 and references therein). Both have invaded South Africa and were collected in this study. Comparisons of impacts based on presence-absence were not made for *A. hortensis*, because it was collected at 21 of the 23 sites sampled; being absent at only one fynbos (Site 26) and one pine plantation (Site 31) site. No mollusc species (either alien or native) was collected at Site 26. This fynbos site was quite dry, exposed and had sparse, dry leaf litter, so may not be suitable in general for molluscs. At Site 31 (pine plantation), only one individual each of two other alien molluscs (*Oxychilus* sp. and cf. *Punctum* sp.) was collected. For some unknown reason, this pine site also appears to be unsuitable for molluscs. Other native forest litter taxa, including millipedes and woodlice, were likewise poorly represented at this site.

Although the slug *D. panormitanum* feeds primarily on plant material, it is aggressive towards other individuals, bites readily and is cannibalistic, even when food is abundant (Herbert, 2010). It is pertinent to note that no native slug species was collected in this study. Furthermore, in this study, *D. panormitanum* abundance was positively and significantly correlated with both native snail species richness and abundance across habitats. Mean native snail species richness and abundance were also significantly higher at sites where *D. panormitanum* was present. While this suggests that *D. panormitanum* does not negatively impact the native mollusc fauna, it more likely implies that certain sites and habitats (namely forest) are more attractive to molluscs, whether native or alien. Alien slugs may further impact the native fauna by outcompeting them for moisture-retaining spaces under rocks, logs and in ground surface depressions; especially during the summer dry season (Mahlfeld, 2000).

*Oxychilus draparnaudi* readily eats other land snails in captivity, and appears to have reduced the numbers and diversity of large native snail species in Iowa, more likely as a

consequence of carnivory than competition for food (Frest & Rhodes, 1982). *O. draparnaudi* has also been identified as the most serious introduced predator of native terrestrial snails in New Zealand, threatening at least two rare species with extinction (Mahlfeld, 2000). In South Africa, the native dwarf cannibal snails, *Nata tarachodes* and *N. vernicosa*, prey on smaller native snails (such as *Trachycystis* spp.) and on earthworms (Herbert & Kilburn, 2004). This suggests that the native snail fauna of the Cape Peninsula is not entirely naïve to, and may be able to tolerate or avoid, alien cannibal snails such as *O. draparnaudi*. No significant correlation of native snail species with alien abundance, or difference in mean native snail species richness or abundance, was found for *O. draparnaudi*. The observed reductions in native snail richness and abundance where this species occurred in each habitat may prove statistically significant with a larger sample size and parametric statistics. *O. draparnaudi* is relatively abundant in natural habitats around Cape Town (Herbert, 2010), so numbers and potential impact should be monitored carefully. There are enough examples around the world of the devastating impacts of successfully introduced molluscs to take this threat seriously (Mahlfeld, 2000).

If the Portuguese millipede, *Ommatoiulus moreleti*, does have an impact on the Cape Peninsula, juliform (worm-like) native millipede species are probably worst affected, because they are morphologically and behaviourally most similar to Portuguese millipedes, and might thus experience interference competition. However, in light of the significant positive correlations recorded here, millipedes may simply congregate in suitable microhabitats, with little or no interaction between species. *O. moreleti* was collected at all 23 sites sampled, so comparisons of potential impacts between sites based on presence-absence cannot be made. Portuguese millipedes were also far more abundant than any native millipede, and 2.6 times more abundant than all native millipedes combined across sites. Portuguese millipedes typically quickly reach high abundance at invaded sites (Baker, 1985; McKillup *et al.*, 1988; Stoev *et al.*, 2010).

Collembola are often the most abundant terrestrial arthropods, many species have cosmopolitan distributions, and several have become invasive (Zettel, 2010). *Entomobrya nivalis* and *Tomocerus minor* were collected at a single site each, so the impacts of these springtails on the native fauna could not be calculated. *T. minor* had not previously been recorded in South Africa, so it may either have only recently invaded the Cape Peninsula, or have simply never been collected. It is known from a single pine plantation (Site 15, Cecilia), which has been clear-felled since sampling. *Neanura muscorum* was collected at four sites, and showed a significant correlation with native springtail richness ( $R = 0.545$ ,  $p = 0.007$ ), and higher mean native species richness occurred at sites where it was present ( $Z = -2.433$ ,  $p =$

0.009). These springtails are not known or expected to have serious detrimental impacts on native springtails, or on other invertebrates (Coates, 1968). They feed mainly on decaying organic matter and associated microorganisms, and are therefore not considered pests (Zettel, 2010). However, as detritivores, alien springtails may have significant effects on decomposition processes (Greenslade, 2002), and indirectly impact other detritivores.

The abundance of European wasps (*Vespa germanica*) was positively and significantly correlated with the abundance of native wasps in both forest and pine plantation. These positive correlations could reflect selection for Lepidoptera larvae-rich areas, since many wasps are predators or parasites of Lepidoptera. Sackmann *et al.* (2008) experimentally showed that *V. germanica* did not affect arthropod assemblages in north-west Patagonia, Argentina. Although their finding contradicts previous studies elsewhere, Sackmann *et al.* (2008) suggest that the low population levels of European wasp, relative to those in other invaded regions, might explain these findings. European wasp numbers collected in this study were also very low. The reported impacts on arthropods are more severe when European wasps switch from small annual colonies to large perennial colonies, as has been demonstrated in Hawaii (Wilson *et al.*, 2009). The climatically marginal conditions of fynbos (Tribe & Richardson, 1994) may have prevented European wasps from switching to large perennial colonies on the Cape Peninsula. However, this colony switch cannot be ruled out in the future, should European wasps undergo range expansion during wetter periods to invade the moister east coast of South Africa.

The composition of native snail, millipede, woodlouse, springtail and wasp communities does not appear to have been influenced by the presence-absence of an alien species in each respective invertebrate taxon. In Europe, no ecological impacts have been documented for alien spiders (Nentwig & Kobelt, 2010), myriapods (Stoev *et al.*, 2010), terrestrial crustaceans (Cochard *et al.*, 2010), springtails (Zettel, 2010), bugs (Heteroptera) (Rabitsch, 2010) or flies (Skuhrová *et al.*, 2010). The literature supports evidence that some invasions in fact increase species diversity (Hulme, 2003). However, correlation does not imply causation. The most productive habitats may support both the highest proportion of alien species and the highest species richness of native species. This would explain correlated native and alien spider diversity in California (Burger *et al.*, 2001), and is the most parsimonious interpretation of the observed positive correlations between various alien species and their taxonomic equivalents here. For most taxa, vegetation or habitat type, rather than the presence of an alien species, was the most parsimonious explanation for community similarity.

It remains a scientific curiosity why some alien species persist for decades in low numbers at a given location without spreading (Nentwig & Josefsson, 2010). In this study, *Limax*

*maximus* appears to be such a curiosity, having persisted in a single patch of forest for over a century (Herbert, 2010). Most of these alien species were introduced to South Africa many decades ago, and some centuries ago (Table 4.1), with 15 first recorded in South Africa prior to 1970. Those recorded more recently (*O. moreleti*, *V. contracta* and *T. minor*) were probably misidentified, not collected, or not described in the literature until recently. A long naturalised residency time on the Cape Peninsula can also be generally expected, since all 18 non-ant alien species have a mostly European origin, promoting their establishment in the temperate, Mediterranean climate of the Western Cape. With the establishment of pine plantations on the Cape Peninsula in the 1880s, a number of these alien invertebrate species are likely to have been accidentally introduced at the same time, being brought into the country in potted soil. There are various possible reasons for the low numbers of several of the alien species collected and some may still be in the lag phase of invasion, showing little or no increase in abundance or spread (Crooks, 2005; Aikio *et al.*, 2010). *Limax maximus* for example may even be stuck in lag phase, not having spread in over a hundred years since it was first recorded on Table Mountain.

No quantified, systematic and comprehensive survey of terrestrial alien invertebrates has been conducted on the Cape Peninsula, or anywhere else in South Africa, prior to this study. Consequently, no analyses of temporal trends in alien abundance and distribution are possible, given the absence of baseline data. Alien species may be kept under control by native species, as in the case of Portuguese millipede, which is controlled by a native rhabditid nematode in Australia (McKillup *et al.*, 1988). Alien species (e.g. European wasp) may show annual variation in population size, with the annual impact on the native fauna fluctuating accordingly. This study was not designed to provide evidence for lag phases, control by native species, or annual fluctuations in alien populations. Nevertheless, logic dictates that the impact of an alien species is proportional to its abundance (Parker *et al.*, 1999). Based on the 'Ten's Rule', there is also a very low probability that the alien species collected are all high-impact invaders (Williamson & Fitter, 1996; Ricciardi & Kipp, 2008).

### *Conclusion*

The comparative approach adopted here provides no evidence for the displacement and impoverishment of native ground-dwelling ant or other invertebrate communities consistent with the findings in relation to Argentine ant invasions reported elsewhere. Neither ant functional group nor co-occurrence patterns appear to be altered in the presence of Argentine ants. Argentine ant invasion on the Cape Peninsula does not appear to have negatively impacted native ant or other invertebrate communities. Habitat structure and disturbance history offers a

more parsimonious explanation for the trends observed. Several of the impacts observed may be influenced by habitat heterogeneity, especially in fynbos. Findings often vary among studies due to different durations and levels of invasion, disturbance history, habitat variability, compositional differences in the original communities, or simply due to the bias inherent in various sampling methods.

Finding an alien species in a non-invasive state does not of course mean that it cannot become invasive and cause severe ecological impact in the future (Nentwig & Josefsson, 2010). Thus, a precautionary approach is necessary in light of the apparent lack of impact of these 19 alien species, especially given the high levels of local invertebrate endemism found on the Cape Peninsula (Picker & Samways, 1996). The potential loss of endemics resulting from invasion has obvious implications for biodiversity conservation in a national park which has World Heritage status and global biodiversity significance. The potential for future invasions by other alien species also cannot be ruled out, and is heightened by increasing globalisation, international trade, and associated human-assisted transportation of species. This study provides a baseline against which future changes in abundance, distribution, composition and impacts of alien invertebrates on the Cape Peninsula can be compared.



## **CHAPTER 5. ANTS AS INDICATORS OF RESTORATION PROGRESS FOLLOWING CLEAR-FELLING OF PINE PLANTATIONS IN A MEDITERRANEAN-TYPE ECOSYSTEM**

### **Introduction**

Inventorying and monitoring are two separate tasks with different goals. Inventory, or biodiversity assessment, aims to document as fully as possible the taxonomic and ecological diversity of all, or part of, the biota of an area (Kremen *et al.*, 1993; Basset *et al.*, 2009) and can hence be accomplished with a single set of samples. By comparison, biological monitoring aims to document population changes over time, using repeat sampling (Noss, 1990; Basset *et al.*, 2009). The goal of biological monitoring is to distinguish between human-induced disturbance and natural fluctuations from a baseline state (Andersen, 1997b; 1999). This goal necessitates monitoring control sites in 'pristine' habitats, in addition to sites subject to disturbance (Kremen *et al.*, 1993). Well-designed inventories can thus provide the obligatory baseline data for monitoring (Noss, 1990; Rohr *et al.*, 2007); the purpose of this study.

The value of, and necessity for, inclusion of invertebrates in biodiversity monitoring programmes has been widely promoted (Kremen *et al.*, 1993; Andersen *et al.*, 2004; Rohr *et al.*, 2007). Invertebrates can respond rapidly to environmental changes, because they have short generation times, compared to vertebrates or trees (Kremen *et al.*, 1993). Small body size, low vagility, poor dispersal ability and specific habitat requirements also mean that ground-dwelling invertebrates show stronger patterns of spatial turnover than both vertebrates and flowering plants (Ferrier *et al.*, 1999). Ground-dwelling invertebrates show greater site fidelity than most vertebrates (Kremen *et al.*, 1993; Oliver & Beattie, 1996). Furthermore, invertebrates generally greatly outnumber vertebrates in abundance, species richness and higher taxa diversity, often by orders of magnitude (Kitching, 1999; New, 1999b). This high biomass and diversity both reduces the size, and hence environmental impact, of samples and affords statistical rigor in both inventory and monitoring of invertebrates.

Neither inventory nor monitoring of invertebrates can be exhaustive, due to the difficulty of adequately identifying the full range of taxa present (Kremen *et al.*, 1993). The challenges of generating invertebrate species inventories should not be underestimated (Engelbrecht, 2010). Monitoring programmes accordingly rely on indicator taxa that can be identified, given available resources and personnel, and that respond quickly to environmental change, in ways that are easily measured or observed (Kremen *et al.*, 1993). Invertebrates are usually more difficult to

survey than plants, so their use as indicators can only be justified if they perform better than plants and provide additional (fine-scale) information (Andersen & Sparling, 1997).

For most invertebrate groups, (1) a large proportion of species has not been described or discovered, (2) the distribution patterns of species are poorly or unknown, (3) too few (if any) specialists are available to identify specimens, (4) sampling protocols are not adequately standardised and (5) knowledge of responses to environmental change is limited and often hypothetical, or extrapolated from a few case studies (New, 1999b). Terrestrial invertebrates fall into three broad categories of value as tools for monitoring: well-known, catch-up and black hole taxa (New, 1999a; 1999b). Well-known taxa have a long history of interest, most species are described, their biology is broadly understood and patterns of distribution are reasonably well documented. Examples of well-known taxa include butterflies and dragonflies. Catch-up taxa include many groups of invertebrates for which there is a fair level of knowledge of taxonomy, biology and distribution. With some focussed attention, these catch-up taxa could be elevated to 'well-known' status for conservation value. The distinction between well-known and catch-up taxa differs among regions. Ants, for example, may be considered well-known taxa in mesic Australia, but catch-up taxa in temperate Australia and other parts of the world. By comparison, black hole taxa have very poorly understood taxonomy, biology and distribution. Consequently, solid ecological interpretation of black hole taxa is difficult or impossible, and these taxa have little proven value as indicators. Black hole taxa, such as nematodes, are best ignored for conservation purposes, especially in light of the limited resources available for invertebrate conservation. Taxa with a high proportion of rare and low abundance species similarly have limited use or relevance for monitoring, due to the low probability of finding them (New, 1999b).

There is often much confusion over what is being indicated (Andersen, 1999), because indicators have been applied in a variety of contexts (*e.g.* Noss, 1990). These contexts include indication of habitat destruction, contamination, modification and rehabilitation, together with vegetation succession, species diversity and climate change (McGeoch, 1998). It is therefore essential to state precisely what the indicator taxa selected are intended to indicate, especially when contexts are related to management actions (Engelbrecht, 2010). Terrestrial invertebrates used to assess general ecological change after disturbances have been referred to as 'ecological indicators' for their ability to demonstrate the impacts of environmental change on biota (McGeoch, 1998). Ecological indicators (the focus of this study) differ from biological indicators (McGeoch, 1998), that are used as surrogates of biodiversity.

Even when there is agreement on what to indicate, it is difficult to know which indicator species to choose (Simberloff, 1998) because there is no single indicator for biodiversity (Duelli

& Obrist, 2003). Choice of indicator based on statements of faith about one's favourite invertebrate group is not enough to validate their use (Andersen, 1999). Demonstration of a chosen indicator's response to disturbance is also not sufficient to validate its reliability as an indicator. Ecological indicators must also genuinely reflect broad ecological change (Andersen, 1999). It is advantageous, although not required, for ecological indicator taxa to have presence-absence patterns that are positively linearly correlated with the species richness of a larger group of organisms (Duelli & Obrist, 2003; Fleishman *et al.*, 2005; Rohr *et al.*, 2007). While this correlation or cross-taxon congruency is often the goal of indicators, it is most effective within taxonomic groups. Cross-taxon congruence should be approached with caution, because the correlation of species richness between pairs of taxa varies taxonomically and geographically (Su *et al.*, 2004; Bilton *et al.*, 2006). Using higher taxa offers better congruency for invertebrates than does cross-taxon comparison (Lovell *et al.*, 2007). However, no single taxon sufficiently indicates the diversity of others, even in well-studied regions (such as tropical forest) and considering a range of taxa (birds, butterflies, flying beetles, canopy beetles, canopy ants, leaf litter ants, termites and soil nematodes) (Lawton *et al.*, 1998). To avoid misinterpretation, true congruency should only be inferred when  $p$ -values are greater than 0.75 (Lovell *et al.*, 2007).

Hammond's (1994) 'shopping basket' approach to indicator selection is widely recommended (*e.g.* McGeoch, 1998) and supported with case studies (*e.g.* Kotze & Samways, 1999). The 'shopping basket' approach selects a set of taxa that each represents the response of taxonomically or functionally closely related taxa, and thereby adequately represents the community as a whole. Widening the taxonomic focus to families or orders has the advantage of unintentionally including representative species in a range of guilds (Basset *et al.*, 2004). This facilitates wider interpretation than is possible for single species indicators. Recommending individual species as indicators has limitations, because those species are seldom suitable outside of the system in which they were tested (Gollan *et al.*, 2010). Nevertheless, individual species can have advantages as indicators in specific cases, acting as 'umbrella' or 'flagship' species, when resources and knowledge needed for more comprehensive analyses are limited.

The use of unidentified morphospecies (*sensu* Oliver & Beattie, 1996) as indicators has limitations for the interpretation of data (Majer, 2009) and is no longer recommended. Morphospecies may have some use for identifying general trends (Snyder & Hendrix, 2008), but can be misleading, especially when males, females and juveniles of individual species are morphologically different and can mistakenly be classified as separate morphospecies (Slotow & Hamer, 2000). Morphospecies have little value as ecological indicators for monitoring, because they overlook potentially important information, such as region of origin (Gollan *et al.*,

2010). Failure to identify alien, and especially invasive, species could also misguide management decisions and unknowingly promote non-native species (Gollan *et al.*, 2010). Alien invertebrates can be used as a measure of restoration success or failure, because the proportion of alien invertebrates is likely to differ between restored and undisturbed sites (Longcore, 2003). Therefore, taxa that can only be identified to morphospecies, and for which the alien fauna is not well known, would not make appropriate, or responsible, indicators.

Ants have been widely used as indicator species, because they are often highly sensitive to disturbance and habitat transformation (Hoffmann & Andersen, 2003). In particular, ants have a long history of use as indicators of restoration success in the mining industry in Australia (*e.g.* Andersen, 1997b) and more recently in South Africa (Majer & De Kock, 1992; van Hamburg *et al.*, 2004). Ant communities respond to disturbance through loss of diversity and through changes in species composition, interspecific interactions, trophic interactions with honeydew-producing hemipterans and ant-plants, and ant-provided ecosystem services, such as seed dispersal (Philpott *et al.*, 2010). Ant assemblages can be reliably assessed on both taxonomic (genera are easily identified) and functional levels (New, 2000). Their functional importance and ease of sampling makes ants effective and efficient taxa for assessment and monitoring in land management (Andersen, 2010).

As with any indicator, the use of ants as ecological indicators relies on the assumption that changes in ant communities reflect ecosystem changes (Andersen, 1999; 2010). This assumption appears to be valid, at least for most relevant studies on ants (Andersen, 2010). However, ants may have limited predictive indicator value when small scale heterogeneity is high, as in grassland ecosystems in Victoria, Australia (New, 2000). In such cases, ants may not be sufficiently sensitive to floristic change to be used as the only indicators for monitoring environmental change. The choice of indicator taxa depends on the monitoring goals set.

Ants and other invertebrates show potential as ecological indicators of restoration progress. Restoration often relies on the assumption that the native fauna associated with a habitat will return as the natural vegetation is re-established (Longcore, 2003; Gratton & Denno, 2005; Majer, 2009; Babin-Fenske & Anand, 2010). This assumption is seldom verified, despite the importance of the re-establishment of trophic interactions among organisms in restored habitats (Gratton & Denno, 2006). The presence of organisms is not sufficient to demonstrate that they adequately perform ecosystem functions in restored habitats (Majer, 2009). Trophic interactions should be monitored explicitly, because they are vital to our understanding of how ecosystems recover (Gratton & Denno, 2006). Different taxa colonise disturbed sites at different rates (Dunn, 2004). In tropical rainforest restoration, for example, invertebrate herbivores and

detrivores recover much faster than predators (Jansen, 1997). This trend relates to different levels of taxa in the food chain, and is therefore probably widespread across habitats. This trend can also be used as a measure of restoration progress. However, there is a distinct paucity of studies on terrestrial invertebrates in the restoration literature. For example, a review of the first 14 years of *Restoration Ecology* revealed that of the 845 papers published, a meagre 12.4% had vertebrates or invertebrates as the main focus (Majer, 2009). Few generalities have been deduced on the use of invertebrates in the restoration process.

The species identity of fauna that return to sites undergoing restoration is important. On mined dunes in Maputaland, South Africa, the dung beetle fauna is dominated by widespread species, whereas natural dune forest that has not been mined supports a high proportion of localised endemic dung beetle species (Davis *et al.*, 2002). While the absence of endemic species at rehabilitated sites is expected, this has implications for biodiversity conservation, and highlights the danger in using species richness as the sole measure of restoration success. For ants and birds in tropical forests, the recovery of species composition takes much longer than the recovery of species richness (Dunn, 2004). This finding is probably broadly applicable to most terrestrial invertebrate taxa in most habitats.

To measure restoration progress, an assessment of the resultant species assemblage is needed (Brewer & Menzel, 2009). Some knowledge of reference condition and at least one extant reference site are advantageous. Restored sites should ideally be compared against a number of reference sites to encompass historically relevant environmental variation. This may not always be possible, or practical, since appropriate reference sites may be extremely rare or no longer exist. Attention should also be paid to off-site species that expanded their distribution into the areas now being restored, but that were not part of the original reference community. Regionally rare off-site species may be negatively affected by restoration efforts, which is of particular concern in biodiversity hotspots.

The Cape Peninsula is renowned for its exceptional diversity and endemism, with 158 endemic angiosperm (Helme & Trinder-Smith, 2006) and at least 111 endemic invertebrate (Picker & Samways, 1996) species recorded in an area of 471 km<sup>2</sup>. The greatest threat to biodiversity on the Cape Peninsula comes from increasing alien plant invasions (Richardson *et al.*, 1996), which are predicted to replace at least 30% of the remaining natural vegetation over the next two decades (Rouget *et al.*, 2003). Removal of commercial pine plantations is akin to clearing invasive alien stands, because pines were originally planted into pristine fynbos (Holmes *et al.*, 2000). Pine plantations also act as the source for many of the alien plant invasions threatening biodiversity on the Cape Peninsula (Richardson *et al.*, 1996). The spread

of invasive alien trees from commercial plantations into adjacent native vegetation threatens conservation areas (Armstrong *et al.*, 1998), requires on-going management intervention, and offers strong motivation for the removal of these old plantations.

Pine plantations on the Cape Peninsula were first established in the 1880s (Cowling *et al.*, 1996; Richardson & Higgins, 1998). Commercial plantations were established in the fynbos surrounding forest patches, but rarely in areas cleared of evergreen native forest (Mucina & Geldenhuys, 2006). Therefore, restoration after clear-felling pine plantations should be aimed towards fynbos, not forest, communities. Today, plantations on the eastern slopes of the Table Mountain range are in Peninsula Granite Fynbos, because Peninsula Sandstone Fynbos was too unproductive to sustain plantations (T. Rebelo pers. comm., 2010). Very few patches of intact Peninsula Granite Fynbos remain to act as source populations of plants and invertebrates colonising clear-felled patches. Sandstone Fynbos, rather than Granite Fynbos, surrounds most plantations and clear-felled stands on the eastern slopes. Therefore, restoration of the majority of clear-felled pine stands back to the exact original vegetation type and associated faunal communities is unlikely. To add to this dilemma, invertebrate community composition (at least of the litter fauna) appears to differ between Granite and Sandstone Fynbos (refer to previous chapters). Regardless of origin, native fynbos invertebrates should, however, be functionally similar enough to maintain ecosystem processes, such as seed dispersal, litter decomposition and nutrient recycling in these restored areas. The re-establishment of these key ecosystem processes is central to most restoration projects (Holmes & Richardson, 1999).

A structurally and functionally representative fynbos plant community can recover from the soil seed-bank alone, following alien clearance and fire in recently-invaded mountain fynbos (Holmes & Marais, 2000). Serotinous proteoid shrubs and other species lacking soil storage of seeds are generally the only species absent in seed-bank restored communities (Holmes, 2002). Fynbos seed-banks are able to survive for over 25 years under stands of alien *Acacia* on the Cape Peninsula, but are severely reduced in both density and species richness (Holmes & Cowling, 1997; Holmes, 2002). By comparison, fynbos seed-banks under pine plantations on the Cape Peninsula are unlikely to still survive, because these plantations have a much longer planting history (sometimes exceeding 100 years) than the invasive *Acacia* stands studied. These commercial pine plantations have also undergone several planting rotations, further compromising viable, dormant seeds. Most fynbos species have short seed dispersal distances, so natural recovery of vegetation through colonisation from surrounding fynbos patches may take several fire cycles (Holmes & Richardson, 1999), translating to several decades.

Local extinction of many fynbos plant species has been reported following invasion by pine (Richardson & van Wilgen, 1986; Richardson *et al.*, 1989). Most fynbos species are unable to withstand shading under pine, although some native geophytes, including *Ornithogalum* and *Moraea*, do persist (Adamson, 1927). This is yet another reason to remove pine plantations in fynbos, so as to minimise and eventually eliminate propagule pressure. Pines have a tendency to form dense thickets and often out-compete fynbos shrubs in areas recovering from fire (Richardson *et al.*, 1994). Most pine seedlings establish in the first two years after fire in fynbos, when native plant cover is low (Richardson & Cowling, 1992). This may also be the case in clear-felled pine, where pine seedlings are among the first plant species to establish (C. Uys pers. obs.). This also implies that the success of restoration depends on follow-up removal of invasive alien plants, especially pine seedlings, within the first few years after clear-felling.

Terrestrial invertebrates have not been identified or tested as ecological indicators in fynbos, although they have been used as indicators of restoration success in other Mediterranean-type vegetation, such as coastal sage scrub in southern California (Longcore, 2003). Therefore, it is important to identify suitable ecological indicator taxa that reflect appropriate recovery of the litter invertebrate fauna, after clear-felling of pine plantation, towards assemblages that are more typical of mature fynbos on the Cape Peninsula.

The aim of this study was thus to identify and test suitable potential ground-dwelling invertebrate taxa for use as ecological indicators for monitoring restoration progress in fynbos. Two hypotheses were tested. The first hypothesis tested whether the community composition of the selected indicator taxon reflects the chronosequence of time-since-felling. It was predicted that the invertebrate community composition of older felled sites (*i.e.* those felled over five years before sampling) would be more similar to fynbos sites than to pine plantation sites. The second hypothesis tested that the indicator species identified from forest, fynbos and pine plantation sites would be reliable indicators when tested using the clear-felled sites. Effective restoration of fynbos is likely to take several decades, and the oldest sites undergoing restoration were less than a decade since clear-felling. Therefore, it was not expected that any of the clear-felled sites would have similar or equivalent invertebrate communities to the mature Sandstone or Granite Fynbos sites. Nevertheless, if the characteristic ecological indicator species identified in the initial selection are in fact good indicators of mature, intact fynbos habitat, then they will still be scored as such when clear-felled sites are added to the comparison.

Considering the many taxonomic challenges associated with terrestrial invertebrates, monitoring programmes should focus on adult stages of reasonably well-collected species (Basset *et al.*, 2009), preferably well-known taxa (New, 1999a; 1999b). Indicator use should

follow a basic two-step process: initial identification, followed by testing the potential indicator taxa (McGeoch, 1998; McGeoch *et al.*, 2002). Guidelines for developing effective and efficient monitoring programmes for invertebrates need to be tested with case studies (*e.g.* Rohr *et al.*, 2007). Ideally, case studies should adopt both coarse- and fine-filter approaches. Monitoring invasive alien species is one such fine-filter approach (Noss, 1990).

## Methods

### *Study sites and collecting methods for indicator selection data*

Ecological indicator taxa were selected from the ground-dwelling invertebrates collected in three habitats over one spring-summer season. Refer to Chapter 2 and Appendix A for the location of the sites sampled and collecting methods used in Western Cape Afrotemperate Forest (n = 8 sites), Peninsula Sandstone and Granite Fynbos (n = 8 sites) and pine plantation (n = 7 sites; Site 11 omitted) in Table Mountain National Park, on the Cape Peninsula. For each of the 23 sites sampled in forest, fynbos and pine plantation, data from the replicates (10 leaf litter, 10 soil, 10 pitfall trap, 10 sugar-baited ant trap and two decayed log samples) were pooled to obtain a single abundance value per species. Refer to Appendix C for a list of the 670 species collected in forest, fynbos and pine plantation.

### *Baseline data for clear-felled sites*

To test the suitability of the selected ecological indicator taxa, eight additional sites in clear-felled pine plantation were sampled at the same time, in the same areas, and following the same collecting procedures adopted in forest, fynbos and pine plantation. Refer to Appendix A for clear-felled site locations and to Appendix C for a list of the 309 species collected there. Clear-felled sites spanned a chronosequence from recently felled (less than one year before sampling) to earlier felled (over five years since felling) sites (Table 5.1 and Fig. 5.1).

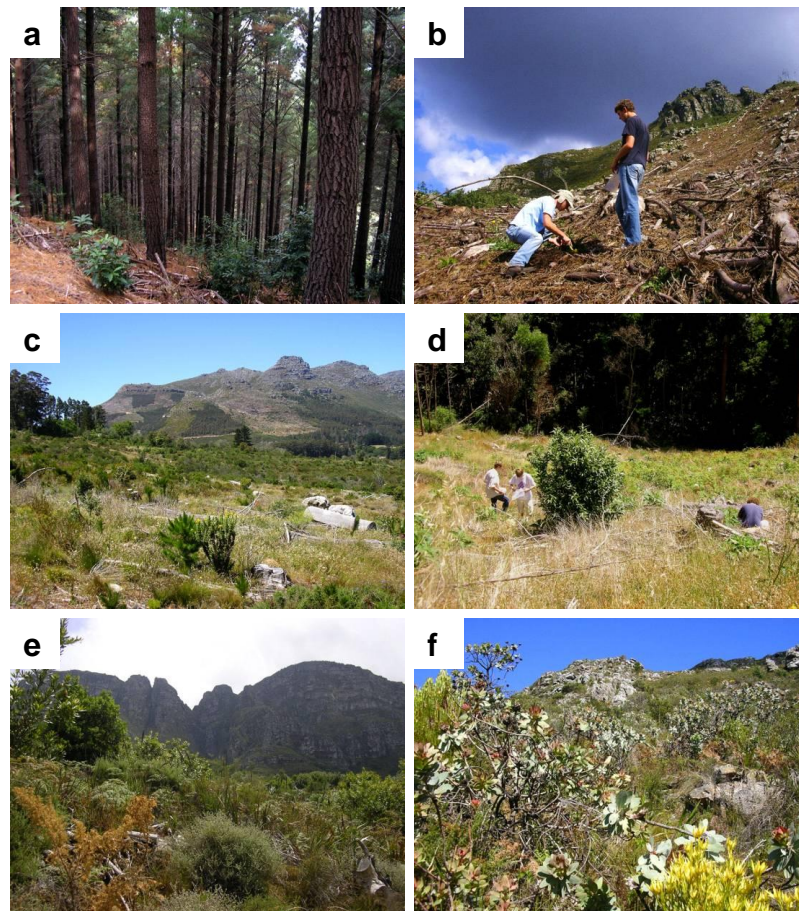
Verification tests of potential indicators should ideally be conducted on an independent data set, either collected in a different area, or at a different time (McGeoch, 1998; McGeoch *et al.*, 2002). However, this is not always possible and depends on the nature of the disturbance. The plantations surrounding Table Mountain National Park targeted for clear-felling by 2025 are in Cecilia and Tokai Plantations. Therefore, a case study on these eastern slopes is appropriate for testing the indicators selected for monitoring restoration progress in fynbos. The indicators selected can be tested in the future once Cecilia and Tokai plantations have all been felled.



**Table 5.1.** Time-since-felling for the clear-felled pine plantation sites sampled in 2008/2009.

Site	Location	Felling date	Chronosequence category
12	Rooikat Ravine, Cecilia	May 2008	recently felled
16	Spilhaus Ravine, Cecilia	April 2008	recently felled
19	Constantia Nek, Cecilia	April 2008	recently felled
20	Constantia Nek, Cecilia	July 2006	over two years since felling
23	Orange Kloof	not confirmed*	over two years since felling
24	Orange Kloof	not confirmed*	over two years since felling
28	Tokai N	July 2007	over one year since felling
32	Tokai S	July 2003	over five years since felling

\* The Section Ranger indicated the number of years since felling. However, Orange Kloof is not part of the current felling schedule, so maps and exact dates were not available.



**Figure 5.1.** Chronosequence of fynbos restoration: (a) mature pine plantation, (b) recently clear-felled, (c) over two years since clear-felling, (d) over five years since clear-felling, (e) recovering Sandstone Fynbos and (f) undisturbed Sandstone Fynbos. Photographs taken during sampling.

### *Indicator selection analyses*

It is impractical to use all invertebrate taxa as ecological indicators for monitoring restoration progress. Therefore, a stepwise approach to indicator selection was adopted. First, taxa were omitted if they were considered incidental catches in this study, because they had extremely low species richness and abundance, or were not ground-dwelling in nature. This step eliminated Hymenoptera (bees only), Thysanura, Neuroptera, Mantodea, Phasmatodea and Thysanoptera from contention as suitable ecological indicators. The remaining ground-dwelling invertebrate taxa were scored using seven criteria that would render them suitable, or unsuitable, as potential indicator taxa. Each taxon was given a final score, calculated as the sum of scores for each of the seven criteria against which taxa were assessed. Final scores could range from zero (worst choice, or most unsuitable) to 14 (most suitable). Taxa were considered unsuitable ecological indicators if they are poorly known regionally, lack taxonomic expertise, are difficult to identify to species level, have either very low or very high species richness, occur in low abundance, are difficult to sample, and/or have few species unique to fynbos (low habitat fidelity). An additional set of criteria for selecting ecological indicators was compiled from the literature. The most suitable potential taxa were subjected to these new criteria to assess current local taxonomic knowledge on a globally relevant scale for monitoring restoration following disturbance.

In addition to the coarse-filter approach of using higher taxa as indicators, a fine-filter approach of monitoring individual species is often recommended, because species may offer more reliable and predictable responses to habitat change (disturbance, restoration, etc.). The indicator value or *IndVal* method developed by Dufrêne & Legendre (1997) is a conceptually straightforward and robust technique for identifying suitable indicator species. *IndVal* combines data on the habitat specificity and fidelity of species, by taking into account the relative abundance of species and number of sites where the species occurs. Indicator species were identified using the programme *IndVal* version 2.1 for Windows, available free online (Dufrêne, 2004).

For each species  $i$  in each habitat  $j$ ,  $A_{ij}$  (the mean abundance of species  $i$  in the sites of habitat  $j$  compared to all habitats sampled) and  $B_{ij}$  (the relative frequency of occurrence of species  $i$  in the sites of habitat  $j$ ) were calculated as follows:

$$\text{specificity measure: } A_{ij} = N_{\text{individuals}_{ij}} \div N_{\text{individuals}_i}$$

$$\text{fidelity measure: } B_{ij} = N_{\text{sites}_{ij}} \div N_{\text{sites}_j}$$

In the formula for  $A_{ij}$ ,  $N_{\text{individuals}_{ij}}$  is the mean number of individuals of species  $i$  across sites of habitat  $j$ , while  $N_{\text{individuals}_i}$  is the sum of the mean numbers of individuals of species  $i$  over all

habitats. The mean number of individuals in each habitat was used, instead of summing the individuals, because this removes any effect of the number of sites in the various habitats, and of differences in abundance among sites belonging to the same habitat.  $A_{ij}$  is maximum when species  $i$  is only present in habitat  $j$ . In the formula for  $B_{ij}$ ,  $N_{sites_{ij}}$  is the number of sites in habitat  $j$  where species  $i$  is present, while  $N_{sites_j}$  is the total number of sites in that habitat.  $B_{ij}$  is maximum when species  $i$  is present in all sites of habitat  $j$ . For each species in each habitat, *IndVal* was then calculated as:

$$IndVal_{ij} = A_{ij} \times B_{ij} \times 100$$

The indicator value of a species for a set of sites is the largest value of *IndVal<sub>ij</sub>* observed over all sites in that habitat. The *IndVal* index reaches a maximum (100%) when the individuals of a species are only recorded in one habitat and in all sites of that habitat. Therefore, species with strong habitat specificity (known as characteristic species) will have the highest index scores and be identified as indicators (Dufrêne & Legendre, 1997). Characteristic indicator species for a habitat are those with significant *IndVal* scores of over 70%. While characteristic species are good indicators of intact habitat, they may not always provide useful information on the direction of ecological change (McGeoch *et al.*, 2002). Species with other combinations of specificity and fidelity (known as detector species) may prove more useful for monitoring habitat changes. Relative changes in the abundance of detector species across ecological states can indicate the direction in which change is occurring. Detector species are those with some degree of habitat preference, identified by *IndVal* scores of between 50% and 70%.

Random reallocation of sites among habitat groups using 499 permutations and five seeds per random number generator was used to test the significance of the *IndVals* for each ant species collected. The significance level was set at  $p < 0.05$ . Good indicator species are those with high and significant *IndVal* percentages. *IndVal* was run for the 17 ant species collected, since ants were selected as the most suitable potential indicator taxon using a coarse-filter stepwise scoring approach. The hierarchy component of Dufrêne & Legendre's (1997) method was not applied, because the habitat levels were known *a priori*. Ant species were tested against forest, pine plantation and the three fynbos 'subtypes' (Sandstone Fynbos, Granite Fynbos and recovering Sandstone Fynbos). *IndVal* was used to identify which species were most characteristic of intact habitats, and which could indicate transitional ecological states (e.g. recovering Sandstone Fynbos) for monitoring restoration progress in fynbos.

#### *Indicator verification analyses*

The indicator taxon selected (ants) was verified by testing the ant community composition response to clear-felling. A Bray-Curtis dissimilarity matrix of log-transformed abundance data was used to map the interrelationships of ant communities in cluster analysis, using complete linkage clustering, and in ordination by non-metric multidimensional scaling (MDS), in PRIMER version 6 (Clarke & Gorley, 2006). Since the aim is to restore these clear-felled sites to fynbos, forest site data were omitted from these community composition analyses. For ants to prove useful as an indicator taxon, they should show progress towards restoration, with older clear-felled sites clustering closer to fynbos sites than to pine plantation sites, thereby displaying more typical fynbos ant communities.

The potential ecological indicator species identified were tested using *IndVal*. All 17 ant species were scored against the felling chronosequence. Since the intention is to restore these clear-felled sites to fynbos, forest site data were omitted from these *IndVal* analyses. Random reallocation of sites among habitat classes using 499 permutations and five seeds per random number generator was used to test the significance of the *IndVals* for each ant species collected. The significance level was set at  $p < 0.05$ .

## Results

### *Indicator selection using a stepwise, coarse-filter approach*

Of the 92 109 individual invertebrates from 670 species collected in forest, fynbos and pine plantation, 27 higher taxa (mostly orders) were collected in sufficient numbers to be considered representative of the ground-dwelling invertebrate community, rather than as incidental catches. Nine additional families from diverse orders (Araneae, Orthoptera, Hemiptera and Coleoptera) were included in this assessment, because they were considered relatively well studied locally. Cockroaches and ants were identified as the most suitable potential ecological indicator taxa for monitoring restoration progress in fynbos (Table 5.2). Ground beetles (Carabidae), assassin bugs (Reduviidae) and darkling beetles (Tenebrionidae) also showed potential as ecological indicators in fynbos (Table 5.2). Ants performed better than cockroaches when subjected to a list of criteria commonly applied to ecological indicator taxa selection for monitoring (Table 5.3).

**Table 5.2.** Criteria for selection or exclusion of invertebrate taxa considered suitable ecological indicators in fynbos. For all criteria, a zero score is the least suitable. Taxa with the highest final scores are considered most suitable as potential ecological indicators for monitoring restoration progress in fynbos.

<b>Taxon</b>	<b>Taxonomic handicap<sup>1</sup></b>	<b>Estimated species richness in fynbos<sup>2</sup></b>	<b>General abundance in fynbos<sup>3</sup></b>	<b>Ease of sampling<sup>4</sup></b>	<b>Species richness in the fynbos sites sampled<sup>5</sup></b>	<b>Total abundance in the fynbos sites sampled<sup>6</sup></b>	<b>Habitat fidelity in the sites sampled<sup>7</sup></b>	<b>Final score</b>
Blattodea (cockroaches)	3	0 (high)	2 (high)	2 (high)	2	2	2	<b>13</b>
Hymenoptera (ants)	3	0 (high)	2 (high)	2 (high)	2	2	0 (very low)	<b>11</b>
Carabidae (ground beetles)	3	1 (medium)	0 (low)	2 (high)	2	1 (low)	1 (low)	<b>10</b>
Reduviidae (assassin bugs)	3	1 (medium)	0 (low)	1 (medium)	1 (too low)	2	2	<b>10</b>
Tenebrionidae (darkling beetles)	2 (well known, identification)	1 (medium)	0 (low)	2 (high)	2	2	0 (very low)	<b>9</b>
Hymenoptera (wasps)	2 (well known, specialist)	0 (high)	2 (high)	1 (medium)	2 (too high)	1 (low)	0 (very low)	<b>8</b>
Araneae (spiders)	2 (well known, specialist)	0 (high)	1 (medium)	1 (medium)	0 (far too high)	2	2	<b>8</b>
Chilopoda (centipedes)	3	1 (medium)	0 (low)	1 (medium)	2	1 (low)	0 (very low)	<b>8</b>
Diplopoda (millipedes)	2 (well known, specialist)	1 (medium)	0 (low)	2 (high)	2	1 (low)	0 (very low)	<b>8</b>
Gastropoda (snails)	3	1 (medium)	0 (low)	2 (high)	1 (too low)	1 (low)	0 (very low)	<b>8</b>
Gryllidae (crickets)	2 (specialist, identification)	1 (medium)	1 (medium)	1 (medium)	1 (too low)	2	0 (very low)	<b>8</b>
Hemiptera (all bugs)	1 (well known)	0 (high)	2 (high)	1 (medium)	1 (too high)	1 (low)	2	<b>8</b>

<b>Taxon</b>	<b>Taxonomic handicap<sup>1</sup></b>	<b>Estimated species richness in fynbos<sup>2</sup></b>	<b>General abundance in fynbos<sup>3</sup></b>	<b>Ease of sampling<sup>4</sup></b>	<b>Species richness in the fynbos sites sampled<sup>5</sup></b>	<b>Total abundance in the fynbos sites sampled<sup>6</sup></b>	<b>Habitat fidelity in the sites sampled<sup>7</sup></b>	<b>Final score</b>
Coleoptera (all beetles)	2 (well known, specialist)	0 (high)	2 (high)	2 (high)	0 (far too high)	2	0 (very low)	<b>8</b>
Collembola (springtails)	1 (specialist)	1 (medium)	2 (high)	1 (medium)	2	1 (low)	0 (very low)	<b>8</b>
Acari (mites)	0	0 (high)	2 (high)	1 (medium)	2	2	0 (very low)	<b>7</b>
Amphipoda (landhoppers)	3	0 (low)	1 (medium)	2 (high)	1 (too low)	0 (very low)	0 (very low)	<b>7</b>
Anostomatidae (king crickets)	3	1 (medium)	0 (low)	1 (medium)	1 (too low)	1 (low)	0 (very low)	<b>7</b>
Diptera (flies)	0	0 (high)	2 (high)	1 (medium)	1 (too high)	2	1 (low)	<b>7</b>
Gastropoda (slugs)	3	0 (low)	0 (low)	2 (high)	1 (too low)	1 (low)	0 (very low)	<b>7</b>
Orthoptera (grasshoppers etc.)	1 (well known)	0 (low)	1 (medium)	1 (medium)	2	2	0 (very low)	<b>7</b>
Scarabaeidae (dung beetles)	3	0 (low)	0 (low)	2 (high)	1 (too low)	1 (low)	0 (very low)	<b>7</b>
Scorpiones (scorpions)	3	0 (low)	0 (low)	1 (medium)	1 (too low)	2	0 (very low)	<b>7</b>
Solifugae (sun-spiders)	3	1 (medium)	0 (low)	0 (low)	1 (too low)	0 (very low)	2	<b>7</b>
Stenopelmatidae (sand crickets)	3	1 (medium)	0 (low)	0 (low)	1 (too low)	0 (very low)	2	<b>7</b>
Lepidoptera (moths)	1 (well known)	0 (high)	2 (high)	0 (low)	1 (unidentified)	1 (low)	1 (unknown)	<b>6</b>
Opiliones (harvestmen)	2 (well known, identification)	1 (medium)	0 (low)	2 (high)	1 (too low)	0 (very low)	0 (very low)	<b>6</b>
Psocoptera (psocids)	1 (specialist)	1 (medium)	0 (low)	1 (medium)	2	1 (low)	0 (very low)	<b>6</b>

<b>Taxon</b>	<b>Taxonomic handicap<sup>1</sup></b>	<b>Estimated species richness in fynbos<sup>2</sup></b>	<b>General abundance in fynbos<sup>3</sup></b>	<b>Ease of sampling<sup>4</sup></b>	<b>Species richness in the fynbos sites sampled<sup>5</sup></b>	<b>Total abundance in the fynbos sites sampled<sup>6</sup></b>	<b>Habitat fidelity in the sites sampled<sup>7</sup></b>	<b>Final score</b>
Archaeognatha (bristletails)	2 (well known, specialist)	0 (low)	0 (low)	0 (low)	1 (too low)	0 (very low)	2	5
Haplotaxida (earthworms)	1 (well known)	1 (medium)	1 (medium)	0 (low)	1 (unidentified)	0 (very low)	1 (unknown)	5
Migidae (trapdoor spiders)	3	0 (low)	0 (low)	0 (low)	1 (too low)	0 (very low)	1 (low)	5
Onychophora (velvet worms)	2 (well known, specialist)	0 (low)	0 (low)	0 (low)	1 (too low)	0 (very low)	2	5
Isopoda (woodlice)	0	0 (high)	0 (low)	1 (medium)	1 (too low)	2	0 (very low)	4
Dermaptera (earwigs)	1 (specialist)	1 (medium)	0 (low)	0 (low)	1 (too low)	0 (very low)	1 (low)	4
Pseudoscorpiones (pseudoscorpions)	0	0 (high)	0 (low)	0 (low)	1 (too low)	2	0 (very low)	3
Tricladida (flatworms)	0	0 (low)	0 (low)	0 (low)	1 (too low)	0 (very low)	0 (very low)	1

<sup>1</sup> Calculated as the sum of three criteria: well-known regionally, specialist identified and/or available, and species level identification possible.

<sup>2</sup> Taxa with either very low or very high species richness in fynbos throughout the region considered unsuitable indicators, based on expert opinion (M. Picker).

<sup>3</sup> Taxa with either very low or very high abundance in fynbos throughout the region considered unsuitable indicators, based on expert opinion (M. Picker).

<sup>4</sup> Refers to practicality of collecting methods required and adequate representation in samples. Rare or difficult to find taxa are considered unsuitable indicators.

<sup>5</sup> Based on data collected in this study and scored as: 1 (too low) if  $\leq 5$  species, 1 (too high) if  $> 25$  species, and 0 (far too high) if  $> 100$  species.

<sup>6</sup> Based on data collected in this study and scored as: low if  $< \frac{1}{2}$  total abundance collected in forest, and very low if  $< 10$  individuals collected.

<sup>7</sup> Based on data collected in this study and scored as: low if most/all species collected in forest and fynbos, and very low if most/all species in all three habitats.

**Table 5.3.** Criteria for using terrestrial invertebrates as ecological indicators for monitoring restoration progress in fynbos following disturbance (clear-felling pine) on the Cape Peninsula.

<b>Suitability criteria</b>	<b>Cockroaches</b>	<b>Ants</b>
Species level identification possible <sup>3,4 *</sup>	Species list in prep.	Unpublished species list available
Distribution, richness and abundance known <sup>3,4 *</sup>	Yes	Yes
Well known taxonomy and life history <sup>2,4 *</sup>	Yes	Yes
Sampling and processing practicality <sup>2,3,5 *</sup>	Fairly high	High
High ecological or habitat fidelity <sup>4 *</sup>	Certain species	Certain species
Sampling and monitoring methods published and used frequently in monitoring <sup>5</sup>	Not used frequently	Pitfall traps and bait cards
Baseline data on biology available <sup>2</sup>	Limited	Fairly good
Functional importance in ecosystems <sup>3</sup>	Decomposition	Wide range
Sensitivity to environmental change <sup>1,3</sup>	Poorly known	Well documented
Distinguish between natural population fluctuations and human induced disturbance <sup>1,2,3</sup>	Requires further study	Functional group predictions possible
Sampled individuals expendable (won't hinder restoration progress) <sup>2</sup>	Yes – few rare species	Yes – most species in large colonies
Representative of related and unrelated taxa <sup>2,3</sup>	Requires further study	Demonstrated elsewhere
Potential for collaboration between researchers and protected area managers <sup>5</sup>	Limited: taxonomists overseas	High: local expertise and interest
Species of special (conservation) concern: IUCN Red List, endemic or other significance <sup>5</sup>	Cape Peninsula endemics	Invasive alien species
Cost efficient (time, funds and personnel) <sup>1,2</sup>	Maybe	Yes

<sup>1</sup> Noss, 1990

<sup>2</sup> McGeoch, 1998

<sup>3</sup> Andersen, 1999

<sup>4</sup> Summerville *et al.*, 2004

<sup>5</sup> McGeoch *et al.*, 2011

\* Assessed in Table 5.2



*Indicator selection using IndVal*

*Pheidole capensis* scored a highly significant *IndVal* of 99.83%, suggesting that it is the most characteristic indicator species in Granite Fynbos (Table 5.4). *P. capensis* was abundant at both Granite Fynbos sites, while absent, or collected in very low abundance (less than five individuals), at the other 21 sites. *Camponotus bertolinii* and *Camponotus* sp. 1 (*maculatus* group) are also potentially good indicator species in Granite Fynbos, with highly significant *IndVals* of 85.39% and 76.51% respectively (Table 5.4). Although all other ant species showed non-significant *IndVals*, *Tetramorium* sp. has potential as an indicator species in Sandstone Fynbos, and *Crematogaster* sp., *Meranoplus* sp. and *Camponotus* sp. 2 (*maculatus* group) have potential as detector species in Granite Fynbos. Interestingly, *Linepithema humile* (Argentine ant) best indicated recovering fynbos, with an *IndVal* of 32.72%.

**Table 5.4.** Indicator values (Dufrene & Legendre, 1997) for the 17 ant species collected in forest, fynbos and pine plantation. Shaded species are potentially suitable as detector species (light grey, *IndVal* 50-70%) or characteristic indicator species (dark grey, *IndVal* > 70%).

Ant species	<i>IndVal</i> (%)	Habitat	Mean	± SD	<i>p</i> (0.05)
<i>Tetramorium grassii</i>	34.60	pine plantation	10.07	0.74	NS
<i>Lepisiota capensis</i>	29.52	pine plantation	19.41	1.08	NS
<i>Tetramorium</i> sp.	70.09	Sandstone Fynbos	19.05	0.94	NS
<i>Camponotus niveosetosus</i>	38.80	Sandstone Fynbos	18.19	0.32	NS
<i>Monomorium</i> sp.	33.77	Sandstone Fynbos	8.14	0.31	NS
<i>Myrmicaria nigra</i>	22.47	Sandstone Fynbos	16.49	0.28	NS
<i>Technomyrmex pallipes</i>	19.24	Sandstone Fynbos	18.37	0.90	NS
<i>Pheidole capensis</i>	99.83	Granite Fynbos	15.89	4.42	**
<i>Camponotus bertolinii</i>	85.39	Granite Fynbos	17.02	2.39	**
<i>Camponotus</i> sp. 1 ( <i>maculatus</i> group)	76.51	Granite Fynbos	15.08	3.07	**
<i>Crematogaster</i> sp.	67.57	Granite Fynbos	15.30	2.10	NS
<i>Meranoplus</i> sp.	58.96	Granite Fynbos	13.63	2.14	NS
<i>Camponotus</i> sp. 2 ( <i>maculatus</i> group)	52.11	Granite Fynbos	16.41	0.00	NS
<i>Tapinoma</i> sp.	41.31	Granite Fynbos	14.26	0.91	NS
<i>Hagensia peringueyi</i>	22.46	Granite Fynbos	15.26	0.39	NS
<i>Tetraponera</i> sp.	35.37	recovering fynbos	14.88	0.08	NS
<i>Linepithema humile</i>	32.72	recovering fynbos	12.31	0.30	NS

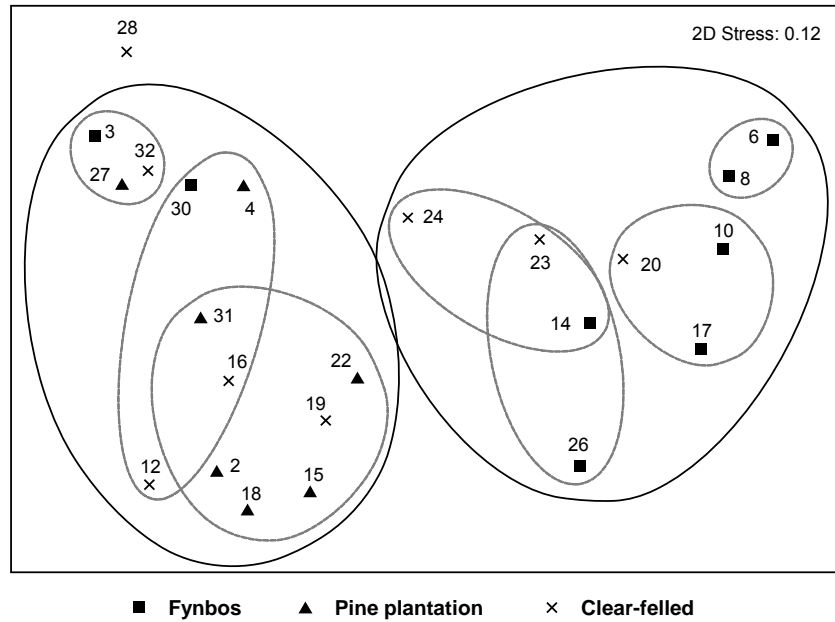
### *Baseline data for clear-felled sites*

In total, 20 295 individual invertebrates representing 309 ground-dwelling invertebrate species were collected at the eight clear-felled sites sampled, 58 of which were unique to clear-felled sites (mostly singletons). This brought the total number of individuals collected in all four habitats to 112 404, representing 728 species. Almost all higher taxa collected at other sites were represented at clear-felled sites. One velvet worm (a single individual of *Peripatopsis stelliporata*), eight spider, one cricket (*Gryllus bimaculatus*), seven bug, 16 beetle, nine fly and 16 wasp species were unique to clear-felled sites. Since ants were the indicator taxon selected, no statistical analyses were performed on other invertebrate taxa for these clear-felled sites.

### *Indicator verification*

Native ant communities were separated into two broad MDS clusters (black circles in Fig. 5.2), with only 22.3% similarity between them, based on the complete linkage cluster analysis. One cluster comprised all mature Sandstone Fynbos (Sites 10, 14, 17 and 26), Granite Fynbos (Sites 6 and 8) and clear-felled sites of over two years since felling (Sites 20, 23 and 24). The other broad cluster comprised all pine plantation sites, recovering fynbos (Sites 3 and 30), recently felled (Sites 12, 16 and 19) and the oldest felled site (Site 32). Clear-felled Site 28 appeared to be an outlier, possibly because baboons destroyed four sugar-baited ant traps and five pitfall traps at this site.

Clusters were further subdivided with 55.5% similarity (smaller grey circles in Fig. 5.2). Granite Fynbos sites (Sites 6 and 8) clustered separately from Sandstone Fynbos and clear-felled sites. The clear-felled site of over two years since felling at Constantia Nek (Site 20) clustered separately from those of a similar age at Orange Kloof (Sites 23 and 24). The three subdivisions within the broad cluster comprising pine plantation, recovering fynbos and other clear-felled sites were not as clearly separated. The three recently felled sites appear to have retained their pine signature, clustering amongst the pine plantation sites. These recently clear-felled sites had sparse ground cover and shrubs, compared to other clear-felled and fynbos sites. By comparison, the oldest clear-felled site (Site 32) had the densest vegetation of all clear-felled sites, was moribund and invaded by tree species and large shrubs not typical of fynbos. As expected, Site 32 clustered close to the recovering fynbos sites.



**Figure 5.2.** Ordination from non-metric multidimensional scaling (MDS), applied to a Bray-Curtis dissimilarity matrix of log-transformed community composition amongst sites for all 17 ant species. Black circles represent 22.3% similarity and smaller grey clusters 55.5% similarity amongst sites.

Of the 17 ant species recorded, only *Tapinoma* sp. was not collected in any of the clear-felled sites. *Pheidole capensis* and *Camponotus bertolinii*, the ant species identified as characteristic indicators of Granite Fynbos, were collected in very low numbers (four and two individuals respectively in total) in clear-felled sites. Both species were again identified as characteristic indicator species in Granite Fynbos, with highly significant *IndVals* of 99.55% for *P. capensis* and 88.83% for *C. bertolinii* (Table 5.5). *Tetramorium* sp. scored a high (albeit non-significant) *IndVal* of 85.43% for clear-felled sites of over two years since felling (Table 5.5). Since *Tetramorium* sp. was previously identified as a potential characteristic indicator species for Sandstone Fynbos (Table 5.4), it must now be rejected as an indicator species for Sandstone Fynbos because of this inconsistent result. *Crematogaster* sp. and *Meranoplus* sp. were still most indicative of Granite Fynbos, but *Camponotus* sp. 2 (*maculatus* group) now best represented Sandstone Fynbos and therefore must also be rejected as an indicator species. *Tetraponera* sp. and *Linepithema humile* (Argentine ant) were again most indicative of recovering fynbos (Table 5.5).

**Table 5.5.** Indicator values (Dufrêne & Legendre, 1997) for the 17 ant species collected in pine plantation, fynbos and clear-felled sites to verify the indicator species previously selected. Shaded species are potentially suitable as characteristic indicator species ( $IndVal > 70\%$ ).

Ant species	<i>IndVal</i> (%)	Habitat	Mean	± SD	<i>p</i> (0.05)
<i>Monomorium</i> sp.	52.28	pine plantation	8.10	2.33	**
<i>Tetramorium</i> sp.	85.43	felled >2 years ago	21.28	1.29	NS
<i>Tetraoponera</i> sp.	32.77	recovering fynbos	17.03	0.25	NS
<i>Linepithema humile</i>	29.95	recovering fynbos	9.60	0.64	NS
<i>Technomyrmex pallipes</i>	61.70	Sandstone Fynbos	23.05	0.74	NS
<i>Camponotus</i> sp. 2 ( <i>maculatus</i> group)	53.09	Sandstone Fynbos	19.35	0.24	NS
<i>Camponotus niveosetosus</i>	46.33	Sandstone Fynbos	18.27	0.09	NS
<i>Lepisiota capensis</i>	31.43	Sandstone Fynbos	17.99	0.95	NS
<i>Myrmecaria nigra</i>	29.44	Sandstone Fynbos	19.19	0.43	NS
<i>Hagensia peringueyi</i>	21.87	Sandstone Fynbos	15.18	0.75	NS
<i>Pheidole capensis</i>	99.55	Granite Fynbos	21.47	2.60	**
<i>Camponotus bertolinii</i>	88.83	Granite Fynbos	20.03	2.00	**
<i>Crematogaster</i> sp.	54.62	Granite Fynbos	17.89	1.00	NS
<i>Camponotus</i> sp. 1 ( <i>maculatus</i> group)	53.83	Granite Fynbos	16.65	1.04	NS
<i>Meranoplus</i> sp.	46.66	Granite Fynbos	17.83	0.50	NS
<i>Tapinoma</i> sp.	41.77	Granite Fynbos	19.17	0.21	NS
<i>Tetramorium grassii</i>	23.02	Granite Fynbos	4.60	0.83	NS

## Discussion

The final scores assigned during indicator selection depend on the criteria chosen and score category range. Several criteria are subjective, while criteria that depend on collected data are influenced by the choice and vagaries of the sites sampled. The rank order of taxa is thus likely to differ, depending on the opinion and experience of the researchers assigning the scores, and on the region in question. Notwithstanding these limitations, this approach, when combined with a case-study to test the selected ecological indicator taxa, is more pragmatic than continuing to ignore or exclude invertebrates in monitoring programmes. Indicator selection criteria can save time and money that might otherwise be wasted studying and monitoring taxa that are not suitable candidates (McGeoch, 1998).

Ants, both as a higher taxon (family) and as individual species, appeared to be the most suitable ground-dwelling invertebrates to use as ecological indicators for monitoring restoration progress in fynbos on the eastern slopes of the Table Mountain range (Tables 5.2-5.5). Ants were recently identified as the most suitable terrestrial invertebrate taxon for inclusion in

protected area monitoring programmes in South Africa (McGeoch *et al.*, 2011). Ants are also by far the most commonly used invertebrate taxon in indicator studies throughout Australia and in parts of North and South America, Europe and Asia (Majer *et al.*, 2007). Compared to most other ground-dwelling invertebrate taxa, ants are easily collected and readily identifiable, making them suitable indicator taxa for monitoring (Andersen & Sparling, 1997; Summerville *et al.*, 2004).

Biodiversity inventories are a vital first step in any monitoring programme (Rohr *et al.*, 2007; Engelbrecht, 2010). Although the species and higher taxon richness was high (728 species across all four habitats), many of the species collected in this study have little value for baseline data for future monitoring, because as morphospecies, they were not identified even to family or genus level. Roughly 20% of the species collected were not checked or identified further by a taxonomic expert, as taxonomists were not available for all taxa collected. Consequently, some unknown degree of identification error was inevitable in these data, with accuracy dependent on prior experience with different taxa and the availability of identification keys. Any error in identifications should, however, be consistent across habitats. Only a fairly low percentage of South African terrestrial invertebrates have been described taxonomically, so taxonomic impediments are inevitable for all but the best-surveyed taxa. This impediment affects community studies involving a range of taxa. The vast majority of invertebrate taxa are too poorly known and difficult to identify to be useful or practical for monitoring (Kremen *et al.*, 1993; New, 1999b).

Despite the taxonomic limitations for other taxa, these baseline data on ant community composition did, to a degree, reflect the chronosequence of time-since-felling. The MDS ordination (Fig. 5.2) suggests that there is restoration progress over time (the ant communities of sites felled over two years previously is more similar to mature fynbos than are recently clear-felled sites). Repeated monitoring of the same sites over time will confirm the suitability of the indicator species selected. However, succession can be hampered if a site is not managed and becomes invaded and dominated by alien plants. Monitoring the relative positions of ant communities in sites undergoing restoration in relation to mature pine plantations and undisturbed fynbos control sites on ordination scatterplots over time can provide a measure of restoration progress (Pik *et al.*, 2002). However, this ant community composition analysis also suggests that vegetation type and age (time-since-felling) alone are insufficient to explain restoration progress in fynbos (Fig. 5.2). The proportions of bare ground, groundcover and shrubs, fire history and presence of invasive alien species, especially Argentine ants, are likely to be equally important drivers of invertebrate community composition. Furthermore, and

contrary to prediction, ant community composition in the oldest felled site (over five years before sampling) was not more similar to fynbos sites than to pine plantation sites. This site would benefit from being burnt, as it is densely invaded by alien grasses and other non-fynbos plants. Clear-felling of pine plantations is only the first stage of rehabilitation on the Cape Peninsula.

The time scale necessary to observe full floral recovery of fynbos after clear-felling is of the order of several fire cycles and thus several decades (Holmes & Richardson, 1999), far beyond the scope of this study, or similar previous studies (e.g. Pryke & Samways, 2009). For this reason, most studies (including this one) adopt the chronosequence approach of comparing sites of different ages at a single point in time in order to infer how succession or colonisation might take place over time. This chronosequence approach has inherent problems, many of which relate to the vagaries of sites (Majer, 2009). As is often the case with biological field studies, uncontrolled factors confounded the interpretation of patterns in these data. For example, baboons destroyed four ant traps and five pitfall traps (almost half of the traps set) at clear-felled Site 28, and one ant trap and two pitfall traps in the adjacent pine plantation Site 27. These sites are consequently not strictly comparable with other, undisturbed fynbos sites, because data from all replicates were pooled to calculate species richness and abundance at each site.

Restoration practitioners often assume that if plant communities are restored, invertebrate communities will return to the undisturbed condition, but this is not always the case (Longcore, 2003; Babin-Fenske & Anand, 2010). Longcore (2003) found that arthropod communities in restored coastal sage scrub in California did not closely resemble arthropod communities at undisturbed sites, regardless of time elapsed since vegetation was established. Instead, restored sage scrub sites were considered “depauperate imitations” that supported lower arthropod diversity and more alien species. Pryke & Samways (2009) found that undisturbed fynbos on the Cape Peninsula supported higher invertebrate species richness than fynbos restoration sites where pine plantations had been removed within the previous five years. Although no significant differences in invertebrate species richness between undisturbed and recovering fynbos were detected in this study, this finding does not imply that restoration is complete, or that invertebrate communities have fully re-established in clear-felled sites. Rather, it emphasises the danger in relying on species richness alone as a measure of restoration progress or success.

This study did not attempt to establish the robustness of the indicator taxa selected by developing and testing appropriate hypotheses under different conditions (different areas or at different times). Exhaustive hypothesis testing defeats the purpose of selecting indicators in the

first place – to save time and money in answering pressing conservation questions (McGeoch, 1998). This study also did not attempt to show correlation between restoration progress and ant species richness, or between ant species richness and the species richness of other invertebrates. While species richness may be an appropriate measure for some taxa, this does not always hold for ants. Ant species richness can remain relatively stable, even when major compositional changes take place (Kaspari & Majer, 2000). Ant species richness can also respond to habitat changes in unpredictable ways that are often case-specific, and therefore difficult to interpret (Andersen, 2010). Most ant-monitoring programmes therefore focus on community composition changes (Kaspari & Majer, 2000; Andersen, 2010). Since ant communities respond to ecosystem disturbance and reflect ecosystem changes, ants are widely used in monitoring faunal changes associated with mine restoration, agriculture and livestock grazing (Andersen, 1997b; 1999; 2010).

Not all of the potential indicator species identified in *IndVal* from forest, fynbos and pine plantation sites (Table 5.4) held as good indicators when tested using the clear-felled sites (Table 5.5). Only those species identified in the initial selection as good indicators of mature, intact fynbos habitat, and that were still scored as such when clear-felled sites were added to the comparison, are recommended for future use in monitoring restoration progress in fynbos. Although this limited the number of candidate indicator species to two (*Pheidole capensis* and *Camponotus bertolinii*), this is not necessarily a problem. Both can be easily and reliably identified to species level, even by non-experts, so these species are well-suited to be incorporated into a rapid assessment monitoring programme in fynbos.

This test of the selected indicator species also highlights the importance of using fine-filter features, such as invasive alien species (Noss, 1990). Habitat disturbance has been shown to facilitate community invasion and subsequent competitive dominance by invasive ants in various ecosystems (Christ, 2009). Argentine ants are known to reduce native ant diversity (e.g. Holway, 1998) and to replace dominant native ants (Bond & Slingsby, 1984). Elsewhere in the fynbos, *P. capensis* is displaced or eliminated by Argentine ants (De Kock & Giliomee, 1989; Christian, 2001; Witt *et al.*, 2004). Therefore, invasion by Argentine ants at sites undergoing restoration could hamper restoration efforts.

At present, undisturbed Granite and Sandstone Fynbos in Table Mountain National Park do not appear to be heavily invaded by Argentine ants. However, Argentine ants were abundant in both recovering fynbos and clear-felled sites (apart from the three most recently felled sites). Pryke & Samways (2009) also recorded significantly higher abundance of Argentine ants in recovering fynbos than in mature fynbos, Afrotemperate forest, or pine plantation on the Cape

Peninsula. They suggest that this may only be temporary, with Argentine ant abundance likely to decline as recovering fynbos sites undergo succession to mature fynbos. Confirmation of this requires regular monitoring, since the invasion and colony establishment of Argentine ants can lead to biotic homogenisation (Holway & Suarez, 2006) and community disassembly (Sanders *et al.*, 2003). In a study of coastal sage scrub restoration, Longcore (2003) concluded that ants were not suitable ecological indicators, because Argentine ants had invaded all sites and reduced native arthropod diversity. However, for this very reason, ants should be considered as indicators. In addition, a goal of restoration should be to eliminate Argentine ants and other alien invertebrates as restoration proceeds, allowing the native community to re-establish.

### *Conclusion*

It will be important to monitor ants over time, at both fine and coarse scales, because invasive alien Argentine ants display a dynamic invasion front, with seasonal and annual fluctuations. Their apparent absence in pristine fynbos in Table Mountain National Park needs to be confirmed, and further researched, as this has implications for their control. Monitoring of restoration progress post-felling should therefore focus on the Argentine ant, *Pheidole capensis* and *Camponotus bertolinii*. The latter two species, verified as characteristic indicators for Granite Fynbos (Table 5.5), should be used for monitoring fynbos restoration progress, because their presence in clear-felled sites could indicate restoration success. Monitoring invasive alien species, especially Argentine ants, is also important in other Mediterranean-climate regions.



## **CHAPTER 6. IMPLICATIONS OF PLANTING AND FELLING PINE FOR GROUND-DWELLING INVERTEBRATES ON THE CAPE PENINSULA**

### **Implications of planting pine for ground-dwelling invertebrates**

This study adds to the growing body of evidence showing that exotic plantations have lower species richness and different community assemblages, compared to neighbouring native forest, in South Africa and globally. These findings follow the global trend of lower biodiversity in plantations compared to natural forests (Stephens & Wagner, 2007). More importantly, alien pine plantations on the Cape Peninsula may also have negative impacts on the fynbos-specialist invertebrate community, whose available habitat has diminished through afforestation. These pine plantations have both direct effects on fynbos invertebrate communities, through habitat-replacement, and indirect effects, through negative on-site and off-site effects.

The pine plantations sampled in this study hold low conservation value in this landscape. Compared to Afrotropical forest and fynbos, pine plantations supported much lower invertebrate abundance, fewer unique species, only one Cape Peninsula endemic species, about the same number of alien invertebrate species, and exhibited lower species turnover (beta diversity). The current pine plantation litter community had a closer resemblance to Afrotropical forest, than to the original Granite Fynbos community, which was displaced by the pine plantations. Community composition results (Chapter 3) suggest that most Granite Fynbos specialist invertebrate species do not survive under pine plantations, and that, due to afforestation, much of the true Peninsula Granite Fynbos invertebrate community may already be lost from this 'Endangered' vegetation type. This likely includes the loss of some Cape Peninsula endemic species, and others that are consequently under threat at the regional scale.

Of the nine Cape Peninsula endemic invertebrate species identified (Chapter 3), the scorpion *Uroplectes insignis* was the only endemic collected in pine plantation, and then only in Newlands Forest. This implies that pine plantations do not provide suitable surrogate habitat for Cape Peninsula endemic species, many of which are Afrotropical forest litter specialists, aquatic or cave-dwelling (Picker & Samways, 1996). These plantations are also not known to harbour any other invertebrate species of conservation concern (*i.e.* IUCN Red Listed species). Plantations often support few forest specialist invertebrate species (Magura *et al.*, 2000), even though they may offer habitat reservoirs for some endangered species (Brockerhoff *et al.*, 2005). While plantations on the Cape Peninsula are known to act as 'surrogate habitat' for components of the native Southern Afrotropical Forest fauna (Ratsirarson *et al.*, 2002;

Raharinjanahary, 2007), they offer only temporary habitat for forest-adapted invertebrates, because plantations are harvested and replanted on a regular basis (roughly every 30-35 years).

Pine plantation is a fairly uniform, artificial habitat, and is dominated by widespread, generalist species, so lower species turnover compared to native habitats was expected and recorded (Chapter 3). High species turnover (beta diversity) for epigaeic invertebrates has previously been reported in fynbos on Table Mountain (Pryke & Samways, 2010), and in Afrotropical forest in the Drakensberg mountains, where turnover ranged from complete to 50%, even between forest patches within the same valley (Hamer & Slotow, 2009; Uys *et al.*, 2009).

### **Implications of alien invertebrate species invasions for native invertebrate taxa**

Invasive alien species are the second leading cause of global biodiversity loss (Wilcove *et al.*, 1998; Simberloff, 2001). Thus, in a National Park of World Heritage Status with globally significant biodiversity, it is a conservation priority to identify alien animals and assess their potential threat to the native biodiversity. The 19 alien invertebrate species identified in this study comprised the Argentine ant (*Linepithema humile*), four slug and eight snail species, the Portuguese millipede (*Ommatoiulus moreleti*), the Rough woodlouse (*Porcellio scaber*), three springtail species, and the European wasp (*Vespula germanica*) (Chapters 3 and 4). This number has almost certainly been underestimated, because most taxa were only identified to morphospecies level and the South African terrestrial alien fauna remains poorly known for most invertebrate taxa (other than ants and molluscs) (Picker & Griffiths, 2011).

Fifteen of the 19 alien invertebrate species were collected in pine plantation, compared to 16 in forest and 11 in fynbos (Chapter 3). Over half of these alien invertebrate species were present in all habitats, and probably represent generalist species. The opportunistic, highly invasive Argentine ant was present at 16 of the 23 sites sampled in all habitats. It is not yet clear whether, or how, Argentine ants, or indeed any of the other alien invertebrate species collected, interact with alien trees to impact native invertebrate diversity.

Unlike for Argentine ants (see Luruli, 2007), most of the distribution and spread data for these 18 non-ant alien invertebrate species in South Africa are anecdotal. This study collected spatial data only, but temporal data are required to investigate the rates of spread of alien invasions. Only one model of potential spread of an alien invertebrate in the Western Cape Province (European wasp: Tribe & Richardson, 1994) has been published. This model may be

outdated, since better data and models of predicted climate change are now available. The model is almost not really applicable to the sites sampled in this study, because it is for spread away from the Cape Peninsula. The model is also unlikely to be applicable to other alien invertebrates, because they differ in their life history traits and environmental tolerances. Particular attention should be paid to carnivorous alien species, including the Brown field slug (*Deroceras panormitanum*), Draparnaud's glass snail (*Oxychilus draparnaudi*) and the European wasp (*Vespula germanica*), each of which could, as they have done elsewhere, potentially negatively impact native invertebrate diversity trophically or through interference competition.

The comparative approach adopted here (Chapter 4) provides no evidence for the displacement and impoverishment of native ground-dwelling ant, or other invertebrate, populations and communities. Argentine ant invasion on the Cape Peninsula does not appear to have negatively impacted native ant or other invertebrate communities. For ants, no clear differences in alpha or beta diversity, functional group composition or co-occurrence patterns were evident with Argentine ant invasion. Similarly, the species richness, abundance and community composition of corresponding native taxa does not appear to be driven by the presence-absence of these 18 non-ant alien species. Habitat structure and disturbance history offers a more parsimonious explanation for the trends observed, particularly in fynbos. Maintaining the natural habitat heterogeneity through appropriate management is thus important for invertebrate conservation in Table Mountain National Park, as well as across the Cape Floristic Region.

### **Implications of felling pine for ground-dwelling invertebrates**

After original vegetation clearing, clear-fell harvesting causes the most extreme disturbance event in plantation forestry (Pawson *et al.*, 2005), especially under intensified forestry and effective fire suppression (Niemelä *et al.*, 1993). Clear-felling radically changes the microclimate conditions of an area in terms of temperature, wind speed, relative humidity, evaporation and solar radiation (Chen *et al.*, 1995). As a consequence, recently (two-year-old) clear-felled sites often temporarily support equal or higher invertebrate species richness than surrounding mature plantations, or native forest (Niemelä *et al.*, 1993; Pawson *et al.*, 2009). This initial elevated species richness is a result of colonisation by open-habitat specialist species, which often dominate clear-fell sites, in addition to the short-term survival of species that colonised the plantation prior to felling (Pawson *et al.*, 2005). While species richness may not be negatively

affected by harvesting, mature forest specialists and especially the litter fauna, often do not persist and fail to recolonise (Niemelä *et al.*, 1993).

Commercial pine plantations in South Africa are mostly planted in 'same age' compartments and clear-fell harvested when mature, with roughly 30-35 years between planting cycles. In Tokai and Cecilia Plantations, the current management plan is to harvest the majority of plantations over a 20-year period up to 2025, and then not to replant them. Management of this land was transferred from Mountain to Ocean (MTO) Forestry Pty (Ltd) to South African National Parks (SANParks) in April 2005, and the land (roughly 1000 ha, of which 600 ha are covered by plantations) has been incorporated into Table Mountain National Park, since this land is of high conservation value (SANParks, 2009).

The ecosystem restoration that is taking place through land acquisition and alien clearing in Table Mountain National Park requires careful monitoring to ensure natural patterns and processes are restored. The time scale necessary to observe full recovery of fynbos after clear-felling of pine plantations spans several fire cycles and hence several decades (Holmes & Richardson, 1999), far beyond the scope of this study, or similar previous studies (*e.g.* Pryke & Samways, 2009b). Therefore, the chronosequence approach (*i.e.* space for time substitution) was adopted, by comparing eight different aged clear-felled sites sampled at the same time, in order to infer how succession or colonisation might take place over time (Chapter 5).

Pine plantations replaced Peninsula Granite Fynbos across the eastern slopes of the Table Mountain range, and the management aim is to restore this 'Endangered' vegetation type. If plantations in areas such as Tokai are not harvested and restored to fynbos, South Peninsula Granite Fynbos could be uplisted to 'Critically Endangered' (SANParks, 2009). The problem is that very little Peninsula Granite Fynbos remains, especially in the southern portion of its distribution, to act as reference sites and a source for the recolonisation of fynbos plants and animals in clear-felled sites at Tokai and Cecilia. Pine plantations have already transformed 13% of Peninsula Granite Fynbos (Rebelo *et al.*, 2006). The target for conservation of 30% is also not met, despite most of this vegetation type falling within Table Mountain National Park and Kirstenbosch National Botanical Garden, because fire-exclusion policies have led to the transformation of much of the conserved fynbos into Afrotropical forest (Rebelo *et al.*, 2006).

Invertebrates should be included in a biodiversity monitoring programme tracking the recovery of fynbos post-felling of pine, because they respond rapidly to environmental change (Kremen *et al.*, 1993; Andersen *et al.*, 2004; Rohr *et al.*, 2007). Ground-dwelling invertebrates are a diverse and functionally important component of the biota, and so should be included in monitoring in their own right, not simply because they are easy experimental subjects.

Moreover, many are short-range (*i.e.* localised) Cape Peninsula endemics. Similarly, many are functionally important in litter decomposition and the release of litter nutrients.

It will be important to monitor ants over time, at both fine and coarse scales, because invasive alien Argentine ants display a dynamic invasion front, with seasonal and annual fluctuations. Mapping the broad distribution of the Argentine ant on the Cape Peninsula would allow for some ecoclimatic modelling, and might provide data on their habitat requirements and altitudinal distribution. This would provide a broader framework for understanding the invasion dynamics in the Cape Floristic Region. In light of the low abundance of Argentine ant in mature fynbos sites compared to other habitats sampled in this study, the putative absence of established nests in mature fynbos in Table Mountain National Park needs to be confirmed, and further researched, as this has implications for their control. Monitoring of restoration progress post-felling should focus on the Argentine ant, *Pheidole capensis* and *Camponotus bertolinii*. These two native species, verified as characteristic ecological indicators for Granite Fynbos (Chapter 5), could be used as benchmarks for monitoring restoration progress, because their presence in clear-felled sites could indicate restoration success. These findings have application throughout the Fynbos Biome and to other Mediterranean-type ecosystems where pine has been introduced and has become invasive. Monitoring alien invasive species, especially Argentine ants, is equally important in other Mediterranean-climate regions.

While the methods adopted identified characteristic species (*P. capensis* and *C. bertolinii*) that could indicate whether restoration is successful, a threshold of abundance would be more convincing as a measure of successful restoration than presence-absence. Further study is required to determine what these thresholds are for each indicator species. Perhaps another way to look at this would be to search for nests of indicator ant species, to ensure that they are resident in sites undergoing restoration, and not simply foraging there temporarily. Thresholds are also likely to be contingent on patch size, habitat heterogeneity and levels of disturbance, including fire history.

Disturbance events are known to facilitate the establishment of invasive species (Hobbs & Huenneke, 1992), in spite of often temporarily increasing species richness. These alien invasive plants and animals can alter the progress and direction of regeneration following disturbance events, such as clear-felling (Pawson *et al.*, 2006). As such, alien invertebrate species merit special inclusion in monitoring programmes (McGeoch *et al.*, 2011), because they can act as a measure of restoration success. The relative proportion of alien invertebrates is likely to differ between restored and undisturbed reference sites (Longcore, 2003). None of the sites sampled in this study can be considered fully restored, but this trend is expected to apply.

Argentine ant invasion could hamper fynbos restoration efforts, because if they displace or prevent native ants from establishing colonies as restoration proceeds, an altered fynbos plant community might result. Tracking co-occurrence patterns of ant communities as restoration proceeds is thus recommended. Argentine ants are known to displace the abundant native ant species involved in the effective dispersal and below-ground storage of large-seeded proteas in fynbos (De Kock & Giliomee, 1989; Christian, 2001; Witt *et al.*, 2004). Thus a goal of restoration should be to control, and if possible eliminate, Argentine ants and other invasive alien species as restoration proceeds. Successful elimination of Argentine ants in fynbos or any other habitat in southern Africa has not yet been achieved. In mature fynbos, control is most likely to be successful if concentrated on open fynbos areas in summer, when low soil moisture levels are expected to be a limiting factor for Argentine ant success.

### **Cautionary notes**

This study was confined to ground-dwelling invertebrates and a small section (about 12 km north-south) of the Cape Peninsula, an area renowned for its exceptional invertebrate diversity and endemism (Picker & Samways, 1996; Hamer & Slotow, 2002; Pryke & Samways 2009a). Results should be interpreted only as an indication of the faunal exchanges that have taken place between exotic pine plantations and native forest and fynbos on the eastern slopes of Table Mountain National Park, and may not apply to plantations in other parts of the Cape Floristic Region, or elsewhere, or to other exotic woody species (*e.g. Acacia, Eucalyptus* and *Quercus* spp.). Nevertheless, the impacts of alien species observed in this study are likely to be more important than in many other regions, owing to the exceptional levels of local endemism on the Cape Peninsula and high beta diversity within and between vegetation types.

Conclusions drawn may also be contingent on the year in which sampling took place. Biotic variations between years resulting from uncontrolled variables, such as precipitation, temperature and competitor/predator pressure, are known to influence community structure (Vaughn & Young, 2010 and references therein). Since sampling was conducted over only one spring-summer season, inter-annual fluctuations in community composition, population demographics and distributions were not accounted for. Therefore, results should be viewed in a short-term context and longer-term changes also need to be monitored. This is especially important for Argentine ants, with their dynamic invasion fronts that result in impacts that vary annually and seasonally.

To have confidence in the validity of findings it is necessary to know the total number of species present in the assemblages sampled, and the number of sampling replicates needed to accurately predict the species richness of an area or habitat (Colwell & Coddington, 1994). Comparative studies of different habitats require a near-complete list of species for each habitat (Thompson *et al.*, 2003). However, there is a trade-off between inventory completeness and sampling intensity (*i.e.* collector effort), and the costs and logistical practicality must be considered. Greater sampling effort may be needed when there is a high proportion of rare species (as in this study), because species accumulation curves are influenced by the proportion of rare species at a site (Thompson *et al.*, 2003).

Capture frequency was low for many of the species collected in this study, with a high proportion of singletons and doubletons. This low abundance (numbers of individuals) and/or low incidence (presence at one or a few sites only) may reflect true rarity, or simply high numbers of 'transient' species that were passing through the area, but were not resident in that habitat. Litter invertebrates are often more vagile than in other assemblages (for example, compared to aerial taxa) and thus expected to show greater turnover between sites (Uys *et al.*, 2009). The slope of the latter part of species accumulation curves for assemblages dominated by rare species is often steeper than for sites or habitats with a more even distribution of relatively abundant species (Thompson & Withers, 2003). This might explain why sampling saturation was not achieved and abundance-standardisation was necessary.

The spatial grain at which species accumulation was investigated might further confound matters. Species accumulation is area dependent, and rarity is often greater at coarser spatial scales (Hui, 2008). Curves were plotted for habitats, with sites used as replicates. Site species counts were calculated by pooling all collecting replicates (leaf litter samples, pitfall traps, etc.) to obtain a single value per site. Therefore, habitat heterogeneity across the spatial extent of sites sampled (12 km north-south distance between furthest sites) may partly account for the lack of sampling saturation in species accumulation curves.

The sampling design was constrained by the pre-defined harvesting plan of the forestry company (MTO). As such, it was not possible to foresee the unplanned felling of pine plantation Site 11 during sampling. As far as possible, pine plantation and clear-felled sites were deliberately chosen in close proximity to forest and fynbos sites, to reduce unwanted spatial variability between treatments and controls. Yet, the 'ideal' scenario of all four habitats in each of the eight areas sampled could not be achieved, and the size and proximity of sites to other habitats varied. These constraints put limitations on the statistical power and interpretation of some findings, but extended the scope and value of this study, especially in fynbos, where both

vegetation type and disturbance history could be compared within fynbos and between habitats. As with many community-type ecological studies, logistical constraints often limit replicate numbers, as was the case here, where site replication was limited by the actual number of existing replicate habitats available.

The findings of this study are broadly compatible with invertebrate survey results in plantations locally (Ratsirarson *et al.*, 2002; Raharinjanahary, 2007; Pryke & Samways, 2009b), regionally (Donnelly & Giliomee, 1985) and world-wide (*e.g.* Stephens & Wagner, 2007). While these findings are naturally most relevant in the Cape Floristic Region, especially on the Cape Peninsula, they are also broadly applicable in Mediterranean-type ecosystems in other parts of the world, especially where pine plantations have replaced native scrubland and thereby threaten native biodiversity.

## Conclusions

As with similar studies in South Africa and globally, this study demonstrates that exotic woody plantations support lower faunal species richness, and different community assemblages, compared to neighbouring native forest, although they support similar species richness to non-forested ecosystems, such as fynbos. Pine plantations, however, appear to be dominated by widespread, generalist species. Plantations may further negatively impact fynbos-specialist invertebrate communities, which have lost habitat through afforestation. Secondly, the strong colonial history associated with plantations on the Cape Peninsula, combined with the mostly European origin of all non-ant alien invertebrates identified here, suggests that these plantations may have facilitated the establishment of some alien invertebrate species. In particular, the carnivorous alien molluscs, European wasp and Argentine ant, require further study and careful monitoring, because the impacts of all alien invertebrates identified were not clear. Argentine ants do not appear to have caused displacement, impoverishment or community disassembly of native ants.

Both planting and felling of alien pine trees impact invertebrate assemblages. Recovery of invertebrate communities post-felling is critical to ensure a functioning ecosystem. Ants show potential as the most suitable ground-dwelling invertebrate taxon to use as an ecological indicator for monitoring restoration progress in fynbos, following clear-felling of pine plantations. Individual ant species (*Pheidole capensis* and *Camponotus bertolinii*) that show potential as characteristic indicators of Granite Fynbos should be monitored as restoration of clear-felled pine sites proceeds.



## The way forward

### *Recommendations for monitoring invertebrates*

- Invertebrate conservation and management needs to be incorporated into mainstream planning and management processes in South African protected areas (Engelbrecht, 2010). McGeoch *et al.* (2011) recommend further surveys in protected areas that focus on alien invertebrate species and their associated impacts, control or eradication, and institution of measures for the prevention of further spread and future invasions.
- The extension, or replication, of a spatially and temporally replicated ant monitoring program, such as the limbovane project (<http://academic.sun.ac.za/iimbovane>), throughout Table Mountain National Park is needed to deliver long-term data (Braschler *et al.*, 2010) and monitor changes as restoration of clear-felled pine proceeds. Valuable lessons can also be learnt from the adoption and implementation of the invertebrate monitoring programme focussed on ants in Kruger National Park, which is also managed by SANParks (McGeoch *et al.*, 2011).
- Long-term monitoring of fixed sites across an altitudinal range (in this case, moving up the mountain, away from the suburbs on the Cape Peninsula) is needed to track the dynamics of the Argentine ant invasion front. Argentine ants are generally not able to sustain colonies in undisturbed fynbos (Macdonald & Jarman, 1984; De Kock & Giliomee, 1989), or in the absence of permanent water sources (Holway, 2005; Parker-Allie *et al.*, 2008), especially at high altitudes (Raharinjanahary, 2007).
- Alien invertebrate species need to be ranked in terms of their impacts, in order to prioritise management actions (Parker *et al.*, 1999). Argentine ants top the list for priority action. Targeted studies for carnivorous molluscs (*e.g.* *Oxychilus* spp.) and the European wasp (*Vespula germanica*) should be extended to include sites outside of the National Park.
- A comparative study of alien invertebrates in other Mediterranean-type ecosystems across the world could advance understanding of invasion pathways and processes, enable early warning systems to be put in place for species that have become invasive elsewhere, and share lessons learnt about impacts and successful eradications. While some of these data are available for well-studied social species, such as Argentine ants and to a lesser degree European wasps, comparative data are urgently needed for other alien invertebrate species.

*Recommendations for monitoring restoration progress in fynbos following clear-felling of pine*

- Clear-felling of pine plantations is potentially beneficial for invertebrate conservation in light of the findings that pine plantations support almost no known Cape Peninsula endemic species and few unique species, yet support a large number of alien invertebrate species in the litter community.
- The challenge will be to document over time whether restoration ultimately leads to the re-establishment of a functional fynbos-specialist invertebrate community, or simply retains an impoverished community dominated by generalist, widespread species.
- Despite the many recognised challenges involved in monitoring with invertebrates (Lovell *et al.*, 2010), the growing number of successful case studies and range of solutions mean that their advantages are beginning to outweigh perceived and real disadvantages (McGeoch *et al.*, 2011). Terrestrial invertebrate indicator taxa hold value and potential for monitoring responses to environmental change in the South African protected area context (McGeoch *et al.*, 2002; Botes *et al.*, 2006a, b; Uys *et al.*, 2010).
- Granite Fynbos is not likely to regenerate satisfactorily without fire, since fynbos is both fire-prone and fire-dependent (Forsyth & Bridgett, 2004). Therefore, active intervention through controlled burning post-felling is necessary. Fynbos-specialist species are most likely fire-adapted and might be disadvantaged, or even excluded, by continued fire suppression.
- The remaining Afrotropical forests, restricted to isolated ravines and fire-protected areas in Sandstone Fynbos, must also be managed and protected during restoration efforts, because they support many of the Cape Peninsula endemic invertebrates (Picker & Samways, 1996) and are a conservation priority (Pryke & Samways, 2009b).
- *Pinus radiata* (Monterey pine) is the most widely planted conifer species for commercial timber production globally (Richardson *et al.*, 1994). It is also highly invasive in Mediterranean-type scrubland vegetation outside of its native range in California (Henderson, 2001). A comparative study of the impacts of planting and felling exotic pine plantations on invertebrate diversity in different Mediterranean-type regions is thus needed.

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**APPENDIX A.** Location of 32 study sites across the eight areas sampled in Table Mountain National Park, on the Cape Peninsula.

Site	Area	Landmark	Altitude (m a.s.l.)	GPS coordinates (WGS 84 Spheroid Standard)		Vegetation
1	Newlands	Above reservoir	230	33° 57' 58.3" S	18° 26' 31.6" E	Afrotemperate forest
2	Newlands	Above reservoir	200	33° 57' 51.9" S	18° 26' 25.1" E	Pine plantation
3	Newlands	Beyond weir	270	33° 58' 17.5" S	18° 26' 23.4" E	Sandstone Fynbos
4	Newlands	Beyond weir	260	33° 58' 24.5" S	18° 26' 27.1" E	Pine plantation
5	Kirstenbosch	Skeleton Gorge	400	33° 58' 55.0" S	18° 25' 25.0" E	Afrotemperate forest
6	Kirstenbosch	Skeleton Gorge	330	33° 59' 03.2" S	18° 25' 28.4" E	Granite Fynbos
7	Kirstenbosch	Nursery Ravine	380	33° 59' 12.6" S	18° 25' 18.7" E	Afrotemperate forest
8	Kirstenbosch	Nursery Ravine	350	33° 59' 17.8" S	18° 25' 19.2" E	Granite Fynbos
9	Cecilia, Rooikat	Rooikat Ravine	400	33° 59' 33.8" S	18° 25' 12.0" E	Afrotemperate forest
10	Cecilia, Rooikat	Rooikat Ravine	430	33° 59' 36.9" S	18° 25' 11.0" E	Sandstone Fynbos
11*	Cecilia, Rooikat	Rooikat Ravine	320	33° 59' 46.0" S	18° 25' 20.8" E	Pine plantation
12	Cecilia, Rooikat	Rooikat Ravine	300	33° 59' 42.9" S	18° 25' 21.6" E	Clear-felled pine
13	Cecilia, Spilhaus	Cecilia Waterfall	400	33° 59' 43.5" S	18° 25' 05.4" E	Afrotemperate forest
14	Cecilia, Spilhaus	Spilhaus Ravine	520	33° 59' 53.7" S	18° 24' 51.6" E	Sandstone Fynbos
15	Cecilia, Spilhaus	Spilhaus Ravine	450	33° 59' 55.7" S	18° 25' 01.4" E	Pine plantation
16	Cecilia, Spilhaus	Spilhaus Ravine	470	34° 00' 03.7" S	18° 24' 45.6" E	Clear-felled pine
17	Constantia Nek	Eagle's Nest	390	34° 00' 23.1" S	18° 24' 17.7" E	Sandstone Fynbos
18	Constantia Nek	Bridle Path	340	34° 00' 15.2" S	18° 24' 46.6" E	Pine plantation
19	Constantia Nek	Bridle Path	330	34° 00' 19.6" S	18° 24' 45.4" E	Clear-felled pine
20	Constantia Nek	Steps	280	34° 00' 31.6" S	18° 24' 19.4" E	Clear-felled pine
21	Orange Kloof	Above weir	130	34° 00' 12.3" S	18° 23' 25.8" E	Afrotemperate forest
22	Orange Kloof	Filtration plant	240	34° 00' 22.8" S	18° 24' 01.6" E	Pine plantation
23	Orange Kloof	Logging road	180	34° 00' 00.6" S	18° 23' 40.2" E	Clear-felled pine
24	Orange Kloof	Logging road	180	34° 00' 18.9" S	18° 23' 45.5" E	Clear-felled pine
25	Tokai N	Boekenhoutkloof	370	34° 02' 17.0" S	18° 23' 44.1" E	Afrotemperate forest
26	Tokai N	Boekenhoutkloof	360	34° 02' 15.9" S	18° 23' 48.8" E	Sandstone Fynbos
27	Tokai N	Boekenhoutkloof	330	34° 02' 23.5" S	18° 23' 53.3" E	Pine plantation
28	Tokai N	Boekenhoutkloof	280	34° 02' 23.1" S	18° 23' 52.5" E	Clear-felled pine
29	Tokai S	Prinskasteel	240	34° 03' 56.1" S	18° 24' 05.4" E	Afrotemperate forest
30	Tokai S	Prinskasteel	310	34° 04' 01.1" S	18° 24' 02.8" E	Sandstone Fynbos
31	Tokai S	Prinskasteel	300	34° 03' 54.3" S	18° 24' 10.2" E	Pine plantation
32	Tokai S	Prinskasteel	230	34° 03' 59.9" S	18° 24' 09.8" E	Clear-felled pine

\* The entire pine block was unexpectedly felled in January 2009, and consequently no pitfall traps, sugar-baited ant traps or decayed logs were sampled.

**APPENDIX B.** Names, institutes and countries of taxonomic experts who assisted with species level identification of selected groups.

<b>Taxon</b>	<b>Name</b>	<b>Institute</b>	<b>City, Country</b>	<b>Pilot</b>	<b>Full-scale</b>
Amphipoda, Isopoda	Charles Griffiths	University of Cape Town	Cape Town, South Africa		*
Araneae (preliminary identification)	Norman Larsen	Iziko South African Museum	Cape Town, South Africa	*	
Araneae: Corrinidae, Salticidae	Charles Haddad	University of the Free State	Bloemfontein, South Africa	*	
Araneae	Ansie Dippenaar-Schoeman	ARC - Plant Protection Research Institute	Pretoria, South Africa	*	*
Blattodea	Horst Bohn	Zoologische Staatssammlung München	München, Germany	*	*
Coleoptera	Peter Hammond	The Natural History Museum	London, England		*
Coleoptera: Pselaphinae	Peter Hlaváč	Private	Košice, Slovakia		*
Coleoptera: Scarabaeoidea	Francois Roets	University of Stellenbosch	Stellenbosch, South Africa		*
Collembola	Ernest Bernard	University of Tennessee	Knoxville, USA		*
Diplopoda	Michelle Hamer	South African National Biodiversity Institute	Pretoria, South Africa	*	*
Diplopoda: Penicillata	Monique Nguyen Duy-Jacquemin	Museum National d'Histoire Naturelle	Paris, France		*
Hemiptera: Cicadellidoidea, Fulgoroidea	Michael Stiller	ARC - Plant Protection Research Institute	Pretoria, South Africa		*
Hemiptera: Reduviidae	Patrick Reavell	University of Stellenbosch	Stellenbosch, South Africa		*
Hymenoptera: Formicidae	Nokuthula Mbanyana	Iziko South African Museum	Cape Town, South Africa		*
Hymenoptera: Amiseginae	Simon van Noort	Iziko South African Museum	Cape Town, South Africa		*
Mollusca	Dai Herbert	Natal Museum	Pietermaritzburg, South Africa	*	*
Oligochaeta	Danuta Plisko	Natal Museum	Pietermaritzburg, South Africa	*	
Onychophora, Coleoptera, Hemiptera, Hymenoptera, Orthoptera	Mike Picker	University of Cape Town	Cape Town, South Africa	*	*
Psocoptera	Charles Lienhard	Museum of Natural History	Geneva, Switzerland	*	*
Scorpiones, Solifugae	Lorenzo Prendini	American Museum of Natural History	New York, USA		*



**APPENDIX C.** Checklist of the 728 species and 112 404 individuals from the 31 sites sampled (Site 11 pine omitted), with the number of individuals in each habitat. C = class, O = order, F = family, SubF = subfamily, A = alien and PE = Cape Peninsula endemic.

Species	Forest	Fynbos	Pine	Felled	
<b>C: TURBELLARIA</b>					
<b>O: Tricladida</b>					
F: Rhynchodemidae					
SubF: Microplaninae					
sp.	34	5	22	2	
<b>C: CLITELLATA</b>					
<b>O: Haplotaxida</b>					
Unidentified	1113	75	263	26	
<b>C: GASTROPODA</b>					
<b>O: Eupulmonata</b>					
F: Arionidae					
<i>Arion hortensis</i> aggregate Férussac, 1819	A	106	29	131	5
F: Agriolimacidae					
<i>Deroceras panormitanum</i> (Lesson & Pollonera, 1882)	A	30	4	3	0
F: Limacidae					
<i>Lehmannia valentiana</i> (Férussac, 1821)	A	28	4	23	3
<i>Limax maximus</i> Linnaeus, 1758	A	2	0	0	0
F: Charopidae					
<i>Trachycystis bisculpta</i> (Benson, 1851)		0	24	0	1
<i>Trachycystis perplicata</i> (Benson, 1851)	PE	6	0	0	0
<i>Trachycystis tollini</i> (Benson, 1856)		32	0	0	0
<i>Trachycystis/ Afrodonta/ alien</i> sp.		13	5	1	0
F: Cochlicopidae					
<i>Cochlicopa</i> sp.	A	16	0	0	0
<i>Cochlicopa</i> cf. <i>lubricella</i> Férussac, 1821	A	56	0	3	0
F: Helicidae					
<i>Cornu aspersum</i> (Müller, 1774)	A	6	0	0	0
F: Hydrocenidae					
<i>Hydrocena noticola</i> Benson, 1856		254	0	0	0
F: Pristilomatidae					
<i>Vitrea contracta</i> (Westerlund, 1871)	A	13	0	19	2
F: Punctidae					
cf. <i>Punctum</i> sp.	A	35	0	38	1
<i>Paralaoma hottentota</i> (Melvil & Ponsonby, 1891)		18	13	6	3
F: Pupillidae					
<i>Lauria cylindracea</i> (da Costa, 1778)	A	0	0	1	0
F: Rhytididae					
<i>Nata tarachodes</i> (Connolly, 1912)		7	0	0	0

Species	Forest	Fynbos	Pine	Felled	
<i>Nata verrucosa</i> (Krauss, 1848)		2	0	0	0
F: Zonitidae					
<i>Oxychilus draparnaudi</i> (Beck, 1837)	A	60	2	13	0
<i>Oxychilus</i> sp. Fitzinger, 1833	A	9	10	10	16
<b>C: ARACHNIDA</b>					
<b>O: Scorpionida</b>					
F: Buthidae					
<i>Uroplectes insignis</i> Pocock, 1890	PE	9	13	6	1
<i>Uroplectes lineatus</i> (C.L. Koch, 1844)		0	9	1	14
<b>O: Pseudoscorpiones</b>					
sp. 1		6	13	3	2
sp. 2		17	0	4	0
sp. 3		0	0	1	1
sp. 4		3	0	0	0
sp. 5		2	1	0	0
<b>O: Solifugae</b>					
F: Solpugidae					
<i>Zeria fusca</i> (C.L. Koch, 1842)		0	7	0	1
<b>O: Araneae</b>					
F: Cyrtaucheniidae					
<i>Ancylotrypa</i> sp. 1		1	1	0	0
<i>Ancylotrypa</i> sp. 2		0	1	0	0
F: Migidae					
<i>Moggridgea quercina</i> Simon, 1903		2	0	1	0
<i>Moggridgea teresae</i> Griswold, 1987	PE	8	1	0	0
F: Nemesiidae					
<i>Hermacha brevicauda</i> Purcell, 1903		3	0	0	0
<i>Hermacha</i> sp.		0	1	0	0
F: Amaurobiidae					
<i>Chresiona</i> sp.		7	1	0	0
F: Anapidae					
sp.		2	2	5	0
F: Araneidae					
<i>Nemoscolus tubicola</i> (Simon, 1887)		0	0	0	1
<i>Neoscona subfusca</i> (C.L. Koch, 1837)		1	0	0	0
F: Clubionidae					
<i>Cheiramiona</i> sp.		1	2	1	1
<i>Clubiona</i> sp. 1		11	2	1	2

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Species	Forest	Fynbos	Pine	Felled
<i>Clubiona</i> sp. 2	4	0	0	0
<i>Clubiona vachoni</i> Lawrence, 1952	1	0	0	0
F: Corinnidae				
sp. 1	1	4	4	3
sp. 2	4	2	0	1
sp. 3	1	0	0	0
sp. 4	1	0	1	0
F: Ctenidae				
<i>Ctenus</i> sp.	0	1	0	0
F: Cyatholipidae				
<i>Cyatholipus quadrimaculatus</i> Simon, 1894	7	2	7	3
F: Dictynidae				
<i>Dictyna</i> sp.	0	1	0	0
<i>Mashimo leleupi</i> Lehtinen, 1967	0	1	0	0
F: Drymusidae				
<i>Drymusa capensis</i> Simon, 1893	3	0	1	0
F: Gnaphosidae				
<i>Asemesthes</i> sp.	0	1	0	0
<i>Camillina</i> sp.	1	2	1	0
<i>Drassodes</i> sp. 1	2	0	0	0
<i>Drassodes</i> sp. 2	1	0	0	0
<i>Zelotes</i> sp. 1	1	2	0	2
<i>Zelotes</i> sp. 2	0	2	0	1
<i>Zelotes</i> sp. 3	0	15	0	10
<i>Zelotes</i> sp. 4	0	0	0	4
<i>Zelowan</i> sp.	0	1	0	0
F: Hahniidae				
<i>Hahnia</i> sp. nov. C.L. Koch, 1841	1	0	0	0
F: Linyphiidae				
<i>Eperigone fradeorum</i> (Berland, 1932)	1	0	0	1
<i>Meioneta</i> sp.	3	0	4	0
<i>Metaleptyphantes</i> sp. 1	17	7	15	7
<i>Metaleptyphantes</i> sp. 2	1	0	1	0
<i>Ostearius melanopygius</i> (OP-Cambridge, 1879)	1	0	0	1
sp. 1	3	2	20	3
sp. 2	1	1	1	1
F: Liocranidae				
sp. 1	0	2	3	0
sp. 2	1	0	0	0
sp. 3	1	0	0	0
F: Lycosidae				
<i>Pardosa</i> sp. 1	0	0	0	2
<i>Pardosa</i> sp. 2	0	0	0	10
sp. 1	0	0	0	9
sp. 2	0	0	0	10
sp. 3	0	2	0	25

Species	Forest	Fynbos	Pine	Felled
F: Mimetidae				
<i>Ero capensis</i> Simon, 1895	2	0	0	0
F: Miturgidae				
<i>Phanotea</i> sp. 1	2	0	0	0
<i>Phanotea</i> sp. 2	1	0	0	0
F: Oonopidae				
<i>Gamasomorpha</i> sp.	1	0	0	0
F: Orsolobidae				
sp.	0	0	1	0
F: Oxyopidae				
<i>Oxyopes</i> sp.	0	2	0	0
F: Palpimanidae				
<i>Palpimanus capensis</i> Simon, 1893	12	0	4	1
F: Philodromidae				
<i>Philodromus vulgaris</i> (Hentz, 1847)	1	4	0	8
F: Pholcidae				
<i>Spermophora gordimerae</i> Huber, 2003	PE	6	3	0
<i>Spermophora peninsulae</i> Lawrence, 1964	PE	1	0	0
<i>Spermophora</i> sp.	4	0	1	0
F: Phyxelididae				
<i>Malaika longipes</i> (Purcell, 1904)	PE	14	2	0
F: Pisauridae				
<i>Atropisaura rothiformis</i> (Strand, 1908)	0	0	1	0
F: Prodidomidae				
sp.	1	0	0	0
F: Salticidae				
SubF: Aelurillinae				
<i>Langona</i> sp.	0	8	0	4
<i>Phlegra</i> sp.	0	1	0	0
sp. 1	0	1	0	0
sp. 2	0	1	0	0
SubF: Euophryinae				
<i>Euophrys</i> sp.	1	2	2	1
<i>Thyenula oranjensis</i> Wesolowska, 2001	8	2	6	2
<i>Thyenula</i> sp. 1	0	0	1	0
<i>Thyenula</i> sp. 2	1	0	0	1
SubF: Heliophaninae				
<i>Heliophanus</i> sp.	0	0	0	3
<i>Natta</i> sp.	0	1	0	0
SubF: Hyllinae				
<i>Evarcha</i> sp.	1	1	3	1
<i>Pellenes</i> sp.	3	2	2	2
SubF: Massagrininae				
<i>Massagris</i> sp.	2	3	3	3
SubF: Plexippinae				
<i>Thyene ogdeni</i> (Peckham & Peckham, 1903)	0	1	0	0

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Species	Forest	Fynbos	Pine	Felled
<i>Thyene</i> sp.	0	2	0	0
sp.	0	2	1	1
F: Scytodidae				
<i>Scytodes gooldi</i> Purcell, 1904	0	1	0	2
<i>Scytodes montana</i> Purcell, 1904	20	17	3	9
F: Segestriidae				
<i>Ariadna</i> sp.	1	1	0	0
F: Selenopidae				
<i>Anyphops</i> sp.	0	4	0	0
F: Tetragnathidae				
<i>Diphya simoni</i> Kauri, 1950	1	0	2	1
<i>Meta</i> sp.	0	0	1	0
F: Theridiidae				
<i>Achaearanea</i> sp.	0	1	3	0
<i>Dipoena</i> sp.	1	5	2	2
<i>Episinus</i> sp.	1	0	0	0
<i>Euryopsis</i> sp. 1	6	76	22	81
<i>Euryopsis</i> sp. 2	0	3	0	1
<i>Steatoda capensis</i> Hann, 1990	4	1	0	2
<i>Steatoda</i> sp.	1	0	0	0
<i>Theridion</i> sp. 1	4	1	1	3
<i>Theridion</i> sp. 2	2	0	1	0
<i>Theridion</i> sp. 3	4	1	0	1
<i>Theridion</i> sp. 4	1	0	2	0
F: Theridiosomatidae				
sp.	1	1	0	0
F: Thomisidae				
<i>Hewittia gracilis</i> Lessert, 1928	0	1	0	0
<i>Monaeses australis</i> (Lawrence, 1937)	1	0	0	0
<i>Oxytate argenteooculata</i> (Simon, 1886)	1	0	0	0
<i>Ozyptila</i> sp.	1	10	0	2
<i>Simorcus haddadi</i> van Niekerk & Dippenaar-Schoeman, 2010	0	1	1	5
<i>Stiphropus</i> sp.	0	2	0	0
<i>Synema abnorme</i> Lessert, 1923	0	0	0	1
<i>Thomisops</i> sp.	0	3	0	0
<i>Tmarus cameliformis</i> Millot, 1941	0	2	0	0
<i>Tmarus foliatus</i> Lessert, 1928	0	2	1	0
<i>Xysticus lucifugus</i> Lawrence, 1937	1	7	1	1
F: Zodariidae				
<i>Akyttara</i> sp.	0	6	0	2
<i>Chariobas cylindraceus</i> Simon, 1893	4	0	0	0
<i>Cydrela</i> sp.	5	0	3	0
<i>Diores simoni</i> O. P.-Cambridge, 1904	1	5	2	8
<i>Diores</i> sp.	0	10	0	1
<i>Diores youngai</i> Jocqué, 1990	0	19	2	15

Species	Forest	Fynbos	Pine	Felled
<i>Heradida</i> sp.	0	3	0	0
<b>O: Opiliones</b>				
sp. 1	702	10	85	52
sp. 2	11	15	5	0
sp. 3	66	11	8	3
sp. 4	10	12	1	0
sp. 5	15	2	2	0
sp. 6	3	0	0	0
sp. 7	4	0	0	0
<b>O: Acari</b>				
sp. 1	56	3	1	2
sp. 2	44	17	3	2
sp. 3	28	7	64	1
sp. 4	35	0	0	0
sp. 5	1	0	4	0
sp. 6	51	2	46	5
sp. 7	0	9	2	1
sp. 8	58	79	159	29
sp. 9	2	99	8	12
sp. 10	59	0	46	1
sp. 11	0	0	1	0
sp. 12	1	0	0	0
sp. 13	3	12	5	0
sp. 14	5	9	22	1
sp. 15	8	0	4	0
sp. 16	8	12	8	6
sp. 17	0	0	1	0
<b>C: MALACOSTRACA</b>				
<b>O: Isopoda</b>				
F: Armadillidiidae				
<i>Armadillidium</i> sp.	37	0	0	0
F: cf. Oniscidae				
sp. 1	54	65	0	11
sp. 2	0	2	0	0
F: Cylisticidae				
<i>Cylisticus</i> sp.	6	3	53	0
F: Porcellionidae				
<i>Porcellio scaber</i> Latreille, 1804	A	49	99	8
sp.	19	0	0	0
F: Trichoniscidae				
<i>Haplophthalmus</i> sp.	18	0	0	0
<b>O: Amphipoda</b>				
F: Talitridae				
<i>Talitriator cylindripes</i> (Barnard, 1940)	1366	143	184	118
<i>Talitriator setosa</i> (Barnard, 1940)	253	25	51	61
<b>C: COLLEMBOLA</b>				

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Species		Forest	Fynbos	Pine	Felled
<b>O: Entomobryomorpha</b>					
F: Entomobryidae					
<i>Entomobrya nivalis</i> (Linnaeus, 1758)	A	0	0	16	2
<i>Entomobrya</i> sp.		0	0	1	1
<i>Lepidocyrtus</i> sp. 1		1	0	2	0
<i>Lepidocyrtus</i> sp. 2		0	9	18	0
<i>Seira barnardi</i> (Womersley, 1934)		1434	32	41	1
<i>Seira capensis</i> Womersley, 1934		35	12	3	0
<i>Seira dayi</i> (Yosii, 1959)		39	30	172	22
<i>Seira ferrarii</i> Parona, 1888		4	5	0	12
<i>Seira nagatai</i> Yosii, 1959		2	0	2	0
<i>Seira</i> sp. 1		9	3	119	5
<i>Seira</i> sp. 2		0	2	0	0
<i>Seira</i> sp. 3		0	5	0	0
<i>Seira</i> sp. 5		3	5	0	8
<i>Seira</i> sp. 6		0	10	0	3
F: Hypogastruridae					
<i>Ceratophysella</i> sp.		0	0	19	0
<b>O: Poduromorpha</b>					
F: Neanuridae					
<i>Neanura muscorum</i> (Templeton, 1835)	A	1	4	2	2
F: Onychiuridae					
<i>Deuteraphorura</i> sp.		0	3	16	0
<i>Orthonychiurus saasveldensis</i> (Weiner & Najt, 1991)		0	0	33	0
F: Tomoceridae					
<i>Tomocerus minor</i> (Lubbock, 1862)	A	0	1	0	4
<b>C: INSECTA</b>					
<b>O: Thysanura</b>					
F: Lepismatidae					
sp.		0	4	0	0
<b>O: Archaeognatha</b>					
F: Machilidae					
<i>Machiloides obsoletus</i> Silvestri, 1904		167	22	7	2
<b>O: Blattodea</b>					
F: Blaberidae					
<i>Aptera fusca</i> (Thunberg, 1784)		0	3	0	0
<i>Perisphaeria, Poeciloblatta</i> sp.		0	8	0	3
F: Blattellidae					
<i>Anallacta confusa</i> Princis, 1963		23	3	0	0
<i>Diptertrum brinckae</i> Princis 1963	PE	0	53	0	0
<i>Ectobius</i> sp. nov.		1	81	3	62
gen. nov.		1	64	1	2
<i>Hoplophoropyga unicolor</i> (Karny, 1908)	PE	0	32	0	30
<i>Temnopteryx phalerata</i> (Saussure, 1864)		13	127	15	90
<i>Xosablatta caffra</i> (Saussure, 1899)		71	4	1	0
F: Blattidae					

Species		Forest	Fynbos	Pine	Felled
<i>Brinckella hanstroemi</i> (Princis, 1949)		0	0	1	0
cf. <i>Duchalluia</i> sp.		4	1	0	4
<i>Pseudoderopeltis</i> sp.		9	21	3	0
<b>O: Mantodea</b>					
sp. 1		1	0	1	0
sp. 2		0	4	0	0
<b>O: Dermaptera</b>					
sp. 1		91	2	53	10
sp. 2		23	0	10	1
sp. 3		18	3	0	1
sp. 4		2	0	1	0
sp. 5		1	0	0	0
<b>O: Phasmatodea</b>					
sp. 1		0	1	1	1
sp. 2		0	12	0	1
<b>O: Psocoptera</b>					
F: Trogiidae					
<i>Cerobasis guestfalica</i> (Kolbe, 1880)		0	0	4	0
gen. nov.		36	10	33	6
<i>Helenatropos abrupta</i> Lienhard, 2005		0	3	8	0
<i>Lepinotus</i> sp.		0	0	1	0
F: Amphipsocidae					
gen. nov.		8	1	0	0
F: Ectopsocidae					
<i>Ectopsocus briggsi</i> McLachlan, 1899		1	1	7	0
F: Pseudocaeceiliidae					
<i>Pseudocaeceilius</i> sp.		1	0	0	0
F: Elipsocidae					
<i>Elipsocus</i> sp.		1	0	1	0
<i>Propsocus pulchripennis</i> (Perkins, 1899)		0	1	1	0
F: Lesneiidae					
<i>Lesneia</i> sp. 1		0	1	0	0
<i>Lesneia</i> sp. 2		0	1	0	0
<b>O: Thysanoptera</b>					
sp.		2	0	0	0
<b>O: Orthoptera</b>					
F: Acrididae					
sp. 1		0	1	0	0
sp. 2		0	8	0	0
sp. 3		0	2	0	3
F: Anostostomatidae					
<i>Henicus brevimicronatus</i> Griffini, 1911		3	0	3	0
<i>Libanasa</i> sp.		4	0	4	0
<i>Onosandridus</i> sp. 1		42	1	1	3
<i>Onosandridus</i> sp. 2		2	4	41	1
sp.		1	16	0	0

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Species	Forest	Fynbos	Pine	Felled
F: Gryllidae				
<i>Cophogryllus</i> sp.	4	61	27	44
<i>Gryllus bimaculatus</i> De Geer, 1773	0	0	0	434
sp.	1	0	0	0
F: Lentulidae				
sp.	0	58	1	0
F: Mogoplistidae				
sp.	96	377	211	767
F: Stenopelmatidae				
<i>Maxentius / Sia</i> sp.	0	3	0	0
F: Tetrigidae				
sp.	0	1	0	0
F: Tettigoniidae				
sp.	1	0	2	0
<b>O: Hemiptera</b>				
F: Miridae				
sp.	0	1	0	0
F: Nabidae				
<i>Prostemma cf. ruficolle</i> Laporte, 1832	0	3	0	1
F: Coreidae				
sp. 1	1	2	0	0
sp. 2	1	0	0	0
F: Anthocoridae				
sp. 1	0	1	0	1
sp. 2	0	0	1	0
sp. 3	1	0	0	0
sp. 4	0	0	3	1
sp. 5	1	0	0	0
sp. 6	0	3	0	3
sp. 7	83	6	21	5
sp. 8	95	0	13	6
sp. 9	0	0	0	1
sp. 10	3	2	0	0
sp. 11	14	0	2	1
sp. 12	4	0	0	0
sp. 13	1	0	0	0
sp. 14	1	0	0	0
F: Enicocephalidae				
sp.	4	0	0	0
F: Lygaeidae				
sp. 1	46	1	0	0
sp. 2	1	0	0	0
sp. 3	1	0	0	0
sp. 4	3	0	1	0
sp. 5	0	0	0	1
sp. 6	0	1	0	1

Species	Forest	Fynbos	Pine	Felled
sp. 7	1	2	0	1
sp. 9	0	7	0	2
sp. 10	54	1	1	28
sp. 11	1	0	0	0
sp. 12	0	1	0	0
sp. 13	0	2	0	1
sp. 15	0	2	0	1
sp. 16	2	1	0	1
sp. 17	16	1	8	2
F: Cydnidae				
sp. 1	0	2	0	0
sp. 2	1	1	1	0
sp. 3	0	1	1	0
F: Pyrrhocoridae				
sp. 1	2	0	0	0
sp. 2	3	5	0	0
F: Reduviidae				
<i>Acanthaspis ehrenberghii</i>	15	0	0	0
<i>Baebius</i> sp. nov.	1	0	0	0
<i>Bargylia</i> sp.	2	0	0	1
<i>Cleptria rufipes</i> Stal, 1856	10	12	44	14
<i>Ploearia</i> sp.	0	1	0	0
<i>Rhynocoris rufus</i> (Thunberg, 1822)	0	5	0	3
<i>Tinna picta</i> Wygodzinsky, 1958	1	4	0	2
cf. <i>Tinna</i> sp.	2	0	0	0
F: Tingidae				
sp. 1	0	0	1	0
F: Aphididae				
sp. 1	9	14	385	94
sp. 2	2	2	341	3
sp. 3	2	7	15	38
sp. 4	0	1	2	11
sp. 5	5	0	0	0
sp. 6	0	0	1	1
F: Cercopidae				
<i>Sepullia</i> sp.	0	0	0	1
F: Cicadellidae				
<i>Capoideus</i> sp.	0	0	0	1
<i>Chiasmus hyalinus</i> (Evans, 1947)	0	0	0	3
gen. nov.	0	0	0	1
<i>Houtbayana</i> sp.	0	1	0	0
<i>Megaulon</i> sp.	0	0	0	2
<i>Platentomus</i> sp.	0	1	0	0
sp.	2	3	0	0
<i>Typhlocybinae</i> sp. 1	1	0	0	0
<i>Typhlocybinae</i> sp. 2	1	0	0	0

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Species	Forest	Fynbos	Pine	Felled
<i>Tzitzikamaia</i> sp.	0	1	0	1
<i>Xestocephalus</i> sp.	0	2	1	0
F: Cixiidae				
sp. 1	2	0	0	0
sp. 2	5	0	0	0
sp. 3	4	1	0	0
F: Delphacidae				
sp. 1	1	1	0	3
sp. 2	1	0	0	0
F: Fulgoroidea				
sp. 1	0	3	0	1
sp. 3	0	1	0	0
sp. 4	0	4	0	2
F: Issidae				
sp.	0	8	0	2
F: Meenoplidae				
sp. 1	45	0	0	0
sp. 2	1	0	0	0
sp. 4	1	0	0	0
sp. 5	1	1	0	0
sp. 7	0	1	1	0
F: Tropiducidae				
<i>Caffrommatissus trimaculatus</i> Fennah, 1967	0	2	0	6
sp.	0	1	0	0
<b>O: Neuroptera</b>				
sp.	0	0	1	2
<b>O: Coleoptera</b>				
F: Carabidae				
<i>Passalidius</i> sp.	20	14	38	45
<i>Thermophilum</i> sp.	0	2	0	0
sp. 1	22	2	78	14
sp. 2	0	0	59	0
sp. 3	0	0	30	0
sp. 4	4	0	6	1
sp. 5	0	3	1	35
sp. 6	17	0	3	3
sp. 7	1	1	6	0
sp. 8	49	17	3	31
sp. 9	0	0	0	1
sp. 10	1	1	0	0
sp. 11	0	4	0	4
sp. 12	0	0	0	1
sp. 13	5	0	0	0
F: Bostrychidae				
sp. 1	0	0	1	0
sp. 2	1	0	0	0

Species	Forest	Fynbos	Pine	Felled
F: Byrrhidae				
sp.	0	7	1	0
F: Lampyridae				
sp. 1	14	3	25	3
sp. 2	1	0	0	0
F: Cerambycidae				
sp. 1	0	3	0	2
sp. 2	1	4	0	0
sp. 3	1	1	0	0
F: Chrysomelidae				
sp. 1	4	2	1	0
sp. 2	0	3	0	0
sp. 3	0	0	0	1
sp. 4	0	0	0	1
sp. 5	0	0	0	1
F: Cleridae				
sp. 1	0	0	1	0
sp. 2	0	0	0	1
sp. 3	1	0	0	0
F: Anthicidae				
sp. 1	10	4	7	0
sp. 2	31	70	139	41
sp. 3	0	1	0	0
F: Cerylonidae				
sp.	46	765	43	505
F: Ciidae				
sp.	0	2	0	9
F: Coccinellidae				
sp.	0	1	1	0
F: Colydiidae				
<i>Pycnomerus</i> sp.	15	3	2	11
F: Corylophidae				
sp.	0	0	0	29
F: Cryptophagidae				
sp.	3	0	0	0
F: Cucujidae				
sp. 1	5	0	0	0
sp. 2	0	0	0	1
F: Discolomidae				
sp.	15	1	0	1
F: Lathridiidae				
sp.	0	0	4	0
F: Monotomidae				
cf. <i>Europs</i> sp.	5	7	83	25
F: Mordellidae				
sp. 1	1	0	0	0

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Species	Forest	Fynbos	Pine	Felled
sp. 2	1	1	0	0
sp. 3	0	0	0	1
F: Nitidulidae				
cf. <i>Eपुरaea</i> sp. 1	1	0	0	0
cf. <i>Eपुरaea</i> sp. 2	1	0	0	0
cf. <i>Haptoncus</i> sp.	3	0	0	0
cf. <i>Lasiodactylus</i> sp. 1	31	0	16	11
cf. <i>Lasiodactylus</i> sp. 2	0	0	1	0
F: Phalacridae				
sp.	0	1	0	0
F: Salpingidae				
sp. 1	1	25	7	9
sp. 2	0	0	0	2
F: Scaptiidae				
sp.	3	0	0	0
F: Silvanidae				
sp.	3	0	0	0
F: Tenebrionidae				
sp. 1	21	1	33	1
sp. 2	0	4	0	1
sp. 3	0	15	21	12
sp. 4	0	22	46	17
sp. 5	8	9	2	24
sp. 6	14	1	31	3
sp. 7	5	3	5	1
sp. 8	8	7	11	7
sp. 9	9	15	8	5
sp. 10	1	0	0	0
sp. 11	0	0	0	1
sp. 12	1	1	0	0
sp. 14	1	0	0	0
F: Curculionidae				
sp. 1	0	0	17	1
sp. 2	0	0	0	1
sp. 3	0	2	0	0
sp. 4	16	2	3	3
sp. 5	0	0	0	1
sp. 6	0	0	0	1
sp. 7	0	1	0	0
sp. 8	2	0	0	0
sp. 9	0	0	0	1
sp. 10	12	0	0	1
sp. 11	2	1	0	0
sp. 12	7	0	4	1
sp. 13	8	0	5	0
sp. 14	2	0	0	0

Species	Forest	Fynbos	Pine	Felled
sp. 15	1	0	0	0
sp. 16	0	0	1	0
sp. 17	6	1	0	0
sp. 18	5	0	0	0
sp. 19	10	2	2	1
sp. 21	1	0	0	0
sp. 22	0	4	0	1
sp. 23	48	0	0	0
F: Platypodidae				
sp.	0	0	0	1
F: Scolytidae				
sp. 1	0	0	1	7
sp. 2	1	0	10	15
sp. 3	3	0	0	0
sp. 4	1	0	0	2
F: Elateridae				
sp. 1	1	0	1	2
sp. 2	1	0	0	0
sp. 3	6	2	0	0
sp. 4	1	0	1	0
sp. 5	2	1	0	0
sp. 7	2	0	4	1
sp. 8	26	1	1	1
F: Histeridae				
sp.	2	0	1	1
F: Scarabaeidae				
<i>Bohepilissus nitidus</i> Balthasar, 1965	PE	115	0	0
<i>Epirhinus hilaris</i> Peringuey, 1901		35	13	195
sp. 1		1	0	0
sp. 2		1	0	0
sp. 3		12	7	1
sp. 4				4
F: Leiodidae				
cf. <i>Colenis</i> sp.		0	1	0
sp. 2		1	0	0
sp. 3		0	0	1
sp. 4		2	3	0
F: Ptiliidae				
sp.		20	12	9
F: Scydmaenidae				
sp. 1		71	16	29
sp. 2		0	0	2
F: Staphylinidae				
SubF: Aleocharinae				
<i>Leucocraspedina</i> sp.		4	0	0
sp. 1		20	4	12
sp. 2		21	6	19

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Species	Forest	Fynbos	Pine	Felled
sp. 3	55	1	2	0
SubF: Omaliinae				
cf. <i>Xylostiba</i> sp.	0	1	2	1
SubF: Oxytelinae				
<i>Thinodromus</i> sp.	0	1	0	0
SubF: Paederinae				
(Euplectini) sp.	0	1	3	0
(Euplectitae) not complete sp.	0	22	0	0
<i>Neoraffraya</i> sp.	60	12	17	0
<i>Neoraffraya variabilis</i> (Raffray, 1897)	4	2	0	0
<i>Novoclaviger joncooteri</i> Hlaváč, 2006	0	1	0	0
<i>Pselaphaulax</i> sp.	0	0	2	0
<i>Pselaphocerus amicus</i> Raffray, 1898	2	0	0	0
<i>Pselaphocerus</i> sp.	1	0	0	0
<i>Pseudotychus nigerrimus</i> Raffray, 1897	4	1	0	0
<i>Raffraya</i> sp.	2	0	0	0
<i>Raffrayidius</i> sp.	17	4	0	0
<i>Raffrayola</i> sp.	3	0	1	0
sp. 4	13	1	73	4
sp. 5	27	4	40	6
<i>Typhloraffraya</i> sp.	0	1	0	0
unidentified	11	1	4	0
<i>Xenogyna</i> sp.	1	6	1	3
SubF: Staphylininae				
cf. <i>Notolinus</i> sp.	0	1	0	1
<i>Quedius</i> sp.	2	0	14	1
<i>Philonthus</i> sp.	18	0	0	0
SubF: Steninae				
<i>Stenus</i> sp.	0	3	1	0
SubF: Tachyporinae				
<i>Mycetoporus</i> sp.	4	0	2	3
<i>Sepedophilus</i> sp. 1	227	0	9	6
<i>Sepedophilus</i> sp. 2	90	2	17	1
<i>Sepedophilus</i> sp. 3	1	3	0	0
<i>Sepedophilus</i> sp. 4	4	1	1	0
<i>Tachyporus</i> sp.	1	0	0	4
<b>O: Diptera</b>				
F: Asilidae				
sp.	0	0	1	0
F: Calliphoridae				
<i>Lucilia</i> sp.	0	0	1	1
sp.	7	0	0	0
F: Cecidomyiidae				
sp.	1	0	0	0
F: Chironomidae				
sp.	0	2	0	2

Species	Forest	Fynbos	Pine	Felled
F: Dolichopodidae				
sp. 1	0	1	0	0
sp. 2	0	4	0	0
F: Drosophilidae				
<i>Drosophila</i> sp. 1	91	1	7	1
<i>Drosophila</i> sp. 2	47	0	21	2
<i>Drosophila</i> sp. 3	0	1	0	3
<i>Zaprionus</i> sp.	6	0	1	0
F: Heliomyzidae				
cf. <i>Suilla</i> sp.	10	0	0	0
F: Neriidae				
<i>Chaetonerius</i> sp.	1	26	0	0
F: Phoridae				
sp.	298	38	301	39
F: Sciaridae				
sp. 1	0	2	1	0
sp. 2	160	132	218	50
F: Tachinidae				
sp.	0	0	0	1
F: Tipulidae				
sp. 1	3	0	0	0
sp. 2	1	328	0	0
F: unidentified				
sp. 3	1	52	0	2
sp. 6	1	5	70	6
sp. 7	13	1	0	0
sp. 8	0	6	0	1
sp. 9	11	0	0	1
sp. 10	5	0	6	0
sp. 11	6	2	2	1
sp. 12	0	1	2	6
sp. 13	4	11	6	4
sp. 14	13	0	5	0
sp. 15	3	1	0	0
sp. 16	2	1	0	0
sp. 17	0	0	0	3
sp. 18	3	0	0	0
sp. 19	1	0	1	0
sp. 20	4	0	0	0
sp. 21	1	0	0	2
sp. 22	0	1	0	1
sp. 23	0	2	0	0
sp. 24	0	2	4	0
sp. 26	0	2	0	0
sp. 27	0	0	2	0
sp. 28	3	0	0	0



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Species	Forest	Fynbos	Pine	Felled
sp. 29	1	0	0	0
sp. 30	2	0	0	0
sp. 31	1	0	0	0
sp. 32	1	0	0	0
sp. 33	0	0	1	0
sp. 34	0	0	1	0
sp. 35	0	1	0	0
sp. 36	0	0	1	0
sp. 37	1	0	0	0
sp. 38	1	0	0	0
sp. 39	1	1	0	0
sp. 41	1	0	0	0
sp. 42	1	0	0	0
sp. 43	1	0	0	0
sp. 44	1	0	0	0
sp. 45	1	0	0	0
sp. 46	0	1	0	0
sp. 47	1	0	0	0
sp. 48	1	0	0	0
sp. 49	1	0	0	0
sp. 50	0	0	1	0
sp. 51	0	0	1	0
sp. 52	0	0	1	0
sp. 53	0	0	1	0
sp. 54	0	0	0	1
sp. 55	0	0	0	1
sp. 56	0	0	0	1
sp. 57	0	0	0	1
sp. 58	1	0	0	0
sp. 59	0	0	0	1
sp. 60	1	0	0	0
sp. 61	0	2	0	0
sp. 62	0	0	1	0
sp. 63	0	0	1	0
sp. 64	0	0	0	1
sp. 65	0	0	0	1
sp. 66	0	3	0	1
<b>O: Lepidoptera</b>				
unidentified	151	14	8	33
<b>O: Hymenoptera</b>				
F: Mutillidae				
sp. 1	0	1	1	0
sp. 3	0	1	0	0
sp. 4	0	1	0	0
F: Bethyridae				
sp.	0	0	1	0

Species	Forest	Fynbos	Pine	Felled
F: Ichneumonidae				
sp. 1	1	0	0	0
sp. 2	1	0	0	0
sp. 3	0	0	1	0
F: Chalcidoidea				
sp. 1	0	0	0	1
sp. 2	0	0	2	0
sp. 3	0	0	1	0
sp. 4	0	0	1	0
F: Sphecidae				
sp.	0	1	0	0
F: Pompilidae				
sp. 1	0	0	1	0
sp. 2	0	1	1	2
sp. 3	0	0	0	1
sp. 4	0	1	0	0
sp. 5	0	0	0	1
sp. 6	0	1	0	1
sp. 7	0	0	0	1
sp. 8	0	0	0	1
sp. 9	1	0	0	0
F: Braconidae				
sp.	5	1	1	0
F: unidentified				
sp. 24	0	2	0	0
sp. 25	3	9	1	9
sp. 26	28	0	1	0
sp. 27	21	0	5	3
sp. 28	22	0	8	1
sp. 29	12	1	13	1
sp. 30	20	0	3	1
sp. 31	42	5	0	0
sp. 32	2	4	1	3
sp. 33	0	1	4	5
sp. 34	4	3	2	1
sp. 35	5	0	3	0
sp. 36	20	1	0	0
sp. 37	2	0	2	1
sp. 38	1	0	1	4
sp. 39	3	1	2	2
sp. 40	5	0	1	9
sp. 41	6	0	0	0
sp. 42	6	0	1	0
sp. 43	2	0	0	14
sp. 44	0	0	6	0
sp. 45	14	0	1	0

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Species	Forest	Fynbos	Pine	Felled
sp. 46	1	2	0	3
sp. 47	0	1	0	4
sp. 48	1	0	1	2
sp. 49	3	0	1	0
sp. 50	1	0	2	0
sp. 51	0	0	6	0
sp. 52	3	0	0	0
sp. 53	3	0	0	0
sp. 54	3	0	0	0
sp. 55	2	0	2	0
sp. 56	2	0	0	0
sp. 57	2	0	0	0
sp. 58	3	0	0	0
sp. 59	4	0	0	0
sp. 60	2	0	0	0
sp. 61	1	0	1	0
sp. 62	2	0	0	0
sp. 63	0	0	0	2
sp. 64	2	0	0	0
sp. 65	2	0	0	0
sp. 66	0	0	1	1
sp. 67	0	1	0	1
sp. 68	0	2	0	0
sp. 69	0	0	0	2
sp. 70	1	0	0	0
sp. 71	1	0	0	0
sp. 72	0	0	1	0
sp. 73	0	1	0	0
sp. 74	0	1	0	0
sp. 75	0	0	1	0
sp. 76	1	0	0	0
sp. 77	1	1	0	0
sp. 78	0	1	0	0
sp. 79	0	1	0	0
sp. 81	1	0	0	0
sp. 82	1	0	0	0
sp. 83	1	0	0	0
sp. 84	1	0	0	0
sp. 85	1	0	0	0
sp. 86	1	0	0	0
sp. 87	1	0	0	0
sp. 88	2	0	0	0
sp. 89	1	0	0	0
sp. 90	1	0	0	0
sp. 91	1	0	0	0
sp. 92	1	0	0	0

Species	Forest	Fynbos	Pine	Felled	
sp. 93	1	0	0	0	
sp. 94	1	0	0	0	
sp. 95	1	0	0	0	
sp. 96	1	0	0	0	
sp. 98	0	0	0	1	
sp. 99	1	0	0	0	
sp. 100	1	0	0	0	
sp. 101	0	1	0	0	
sp. 102	0	0	1	0	
sp. 103	0	0	1	0	
sp. 104	0	0	0	1	
sp. 105	0	0	0	1	
sp. 106	0	0	0	2	
sp. 107	0	0	0	1	
sp. 108	1	0	0	0	
sp. 109	1	0	0	0	
sp. 110	1	0	0	0	
sp. 111	1	0	0	0	
sp. 112	0	0	1	0	
sp. 113	0	0	0	1	
sp. 114	0	0	0	1	
sp. 115	1	0	0	0	
sp. 116	1	0	0	0	
sp. 117	0	0	0	1	
sp. 118	0	0	0	1	
sp. 119	2	0	0	0	
sp. 120	1	0	0	0	
sp. 121	1	0	0	0	
sp. 122	1	0	0	0	
sp. 123	1	0	0	0	
F: Vespidae					
<i>Vespula germanica</i> (Fabricius, 1793)	A	15	14	3	0
F: Chrysididae					
SubF: Amiseginae					
<i>Obenbergerella aenigmatica</i> Bridwell, 1919		3	10	15	0
<i>Reidia turneri</i> (hairy) Krombein, 1957		26	14	122	8
<i>Reidia turneri</i> (few hairs) Krombein, 1957		38	0	45	0
F: Apidae					
<i>Apis mellifera</i> Linnaeus, 1758		0	1	0	0
F: Halictidae					
sp. 1		0	2	0	0
sp. 2		0	2	0	0
F: Formicidae					
SubF: Dolichoderinae					
<i>Linepithema humile</i> Mayr, 1868	A	15829	4546	5841	6681
<i>Tapinoma</i> sp.		0	757	265	0

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Species	Forest	Fynbos	Pine	Felled
<i>Technomyrmex pallipes</i> (Smith, 1876)	0	1325	13	11
SubF: Formicinae				
<i>Camponotus bertolonii</i> Emery, 1895	54	371	149	2
<i>Camponotus niveosetosus</i> Mayr, 1862	36	742	12	12
<i>Camponotus</i> sp. 1 ( <i>maculatus</i> group)	0	371	0	101
<i>Camponotus</i> sp. 2 ( <i>maculatus</i> group)	595	4360	123	161
<i>Lepisiota capensis</i> (Mayr, 1862)	5	9040	25	4824
SubF: Myrmicinae				
<i>Crematogaster</i> sp.	806	3465	0	393
<i>Meranoplus</i> sp.	281	474	1	116
<i>Monomorium</i> sp.	3089	891	5278	1253
<i>Myrmecaria nigra</i> (Mayr, 1862)	0	284	0	87
<i>Pheidole capensis</i> Mayr, 1862	0	1545	0	4
<i>Tetramorium grassii</i> Emery, 1895	3994	1099	1687	1043
<i>Tetramorium</i> sp.	2109	319	131	1294
SubF: Ponerinae				
<i>Hagensia peringueyi</i> (Emery, 1899)	0	252	0	121
SubF: Pseudomyrmicinae				
<i>Tetraoponera</i> sp.	21	37	21	6
<b>C: DIPLOPODA</b>				
<b>O: Polyxenida</b>				
F: Synexidae				
<i>Phryssonotus</i> sp. nov.	0	7	11	4
F: Polyxenidae				
<i>Propolyxenus</i> sp. nov.	3	1	0	1
<b>O: Sphaerotheriida</b>				
F: Sphaerotheriidae				
<i>Sphaerotherium capense</i> Schubart	4	0	5	0
<i>Sphaerotherium commune</i> Attems, 1928	2	1	1	0
<i>Sphaerotherium</i> sp.	22	3	6	0
<b>O: Polydesmida</b>				
F: Vaalagonopidae				
<i>Hemiphygoxerotes crinitus</i> Attems, 1944	6	2	11	0
F: Dalodesmidae				
cf. <i>Gnomeskelus</i> sp.	0	2	3	0

Species	Forest	Fynbos	Pine	Felled
<b>O: Spirobolida</b>				
F: Pachybolidae				
<i>Centrobolus diagramus</i>	16	0	0	0
<b>O: Spirostreptida</b>				
F: Iulomorphae				
<i>Iulomorpha</i> sp.	291	1	66	70
F: Cambalidae				
<i>Ommatoiulus moreleti</i> (Lucas, 1860)	A	508	152	546
<b>C: CHILOPODA</b>				
<b>O: Geophilomorpha</b>				
sp.	51	21	22	9
<b>O: Lithobiomorpha</b>				
F: Henicopidae				
<i>Anopsobius</i> sp.	38	3	0	4
<i>Paralamyctes</i> sp. 1	10	3	4	0
<i>Paralamyctes</i> sp. 2	4	0	2	0
<i>Paralamyctes</i> sp. 3	2	1	0	0
<i>Paralamyctes</i> sp. 4	5	0	1	0
F: unidentified				
sp. 1	1	0	1	1
sp. 2	5	1	12	10
<b>O: Scolopendromorpha</b>				
F: Cryptopsidae				
<i>Cryptops</i> sp.	6	9	4	0
F: Scolopendridae				
<i>Cormocephalus</i> sp.	12	2	21	7
F: Scutiggerinidae				
<i>Scutiggerina weberi</i> Silvestri, 1903	0	0	7	1
<b>C: UDEONYCHOPHORA</b>				
<b>O: Ontonychophora</b>				
F: Peripatopsidae				
<i>Peripatopsis balfouri</i> (Sedgwick, 1885) spp. complex	6	0	2	2
<i>Peripatopsis stelliporata</i> Sherbon and Walker, 2004	0	0	0	1