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Multi-level impacts of introduced wild boar on Patagonian ecosystems

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To the Graduate Council:

I am submitting herewith a dissertation written by Maria Noelia Barrios Garcia Moar entitled "Multi-level impacts of introduced wild boar on Patagonian ecosystems." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

Daniel Simberloff, Major Professor

We have read this dissertation and recommend its acceptance:

Aimee Classen, Nathan Sanders, Jennifer Schweitzer, Charlie Kwit

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

Multi-level impacts of introduced wild boar on Patagonian ecosystems

A Dissertation presented for the
Doctor of Philosophy
Degree
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Maria Noelia Barrios Garcia Moar

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To Mariano and Emma my beloved family,

and to my parents who supported my career decisions.

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Abstract

Biological invasions are a pervasive global change that threatens biodiversity and the functioning of natural ecosystems, yet most studies focus on population impacts. Furthermore, the effects of invasive species on ecosystems are greatest when they introduce a novel disturbance. In this dissertation I reviewed the impact of wild boar (*Sus scrofa*) on native communities worldwide, identifying research needs. Wild boar overturns extensive areas of vegetation to feed on belowground plant parts, insects and fungi, thus altering native ecosystems integrity. By means of observational and experimental studies I addressed some of the research gaps on the impact of wild boar invasions on native communities and ecosystem functioning in Patagonia, Argentina. I evaluated the impact of wild boar on native plant community composition and structure, on soil properties, and on facilitating further invasion. I found that wild boar significantly alters aboveground ecosystem properties by reducing plant biomass and altering plant community composition. Furthermore, wild boar rooting disturbance significantly reduce litter decomposition rates, while soil properties were influenced by plant community more than by boar rooting disturbance. Lastly, I found that rooting disturbance rather than seed dispersal by wild boar facilitates further invasion by plants. Overall, these findings indicate that wild boar can have profound impacts on native ecosystems.

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CHAPTER I: INTRODUCTION

Introduction

Biological invasions are a pervasive global change that threatens biodiversity and the functioning of natural ecosystems (D'Antonio and Vitousek 1992, Vitousek et al. 1996, Mack et al. 2000, Ehrenfeld 2010, Wardle et al. 2011, Simberloff et al. (*in press*)). Although, there is increasing recognition of the influence of invasive species on aboveground-belowground components and how they interact to control community- and ecosystem-level processes (Wardle et al. 2004), most studies focus on population impacts (Simberloff et al. (*in press*)). Understanding how invasive species alter ecosystem structure and function provides information useful for management or mitigation of their impacts. My dissertation centers on understanding the community and ecosystem consequences of wild boar invasion in Patagonia, Argentina.

Wild boar (*Sus scrofa*) are one of the world's worst pests (Lowe et al. 2000) and now occupy all continents except Antarctica, as well as many oceanic islands (Long 2003). In order to feed on belowground plant parts, fungi, and invertebrates, wild boar overturn extensive areas of vegetation (Baubet et al. 2003). This physical disturbance not only directly affects above- and belowground components of ecosystems and their functioning, but also indirectly contributes to further invasion. In my dissertation, I used observational and experimental approaches to evaluate the impact of wild boar on native ecosystems on a large island in Patagonia, Argentina (Figure I.1). In Chapter II, I review the available literature on the effects of wild boar on native and introduced ecosystems. I found that most of the published literature examines boar effects in their introduced range and little is available from the native distribution. Also, most of the research describes direct effects on plant communities and predation on some animal communities, but less is known about indirect effects on ecosystem functions such as primary productivity, decomposition rates, and nutrient cycling. This review was conducted in collaboration with M.S. Sebastian Ballari and the results are reported in a paper in Biological Invasions in 2012. These findings motivated the research goals in the following chapters. In Chapter III, I explored the impact of wild boar rooting disturbance on plant community composition and structure, as well as on decomposition rates. I found that rooting by boar significantly changes plant community composition and decreases organic matter decomposition rates. Thus, I concluded that wild boar are significantly altering the structure and function of native ecosystems in Patagonia. Decomposition rates are controlled by climate, the decomposer community, and the chemistry of the litter (Ehrenfeld 2010). However, I used the same litter substrate across my experiment, and measurements of soil moisture and temperature showed no differences between rooting and intact areas. Therefore, Chapter IV is devoted to determining the impact of rooting disturbance on soil properties and processes, which might shed light on possible changes in the decomposer community. I measured a suite of soil responses (temperature, water content, pH, C content, N content, extractable P, soil respiration, and N mineralization) in areas affected by rooting disturbance of different ages and also intact and experimentally disturbed patches. Surprisingly, I found no effect of rooting disturbance on any of the soil proprieties and processes measured. Instead, the plant community, rather than rooting disturbance, drives significant soil differences. Thus, future work should address other mechanisms altering decomposition rates. Because disturbance is recognized as a means of promoting invasion (D'Antonio et al. 1999), in Chapter V, I explore whether soil disturbance or seed dispersal by wild boar facilitate further invasion. Using effect sizes as the log-response ratio I found that soil disturbance rather than dispersal promotes both establishment and growth of invasive plants. The results in this chapter are currently under review in the journal Austral Ecology.

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Appendix I: Tables and Figures

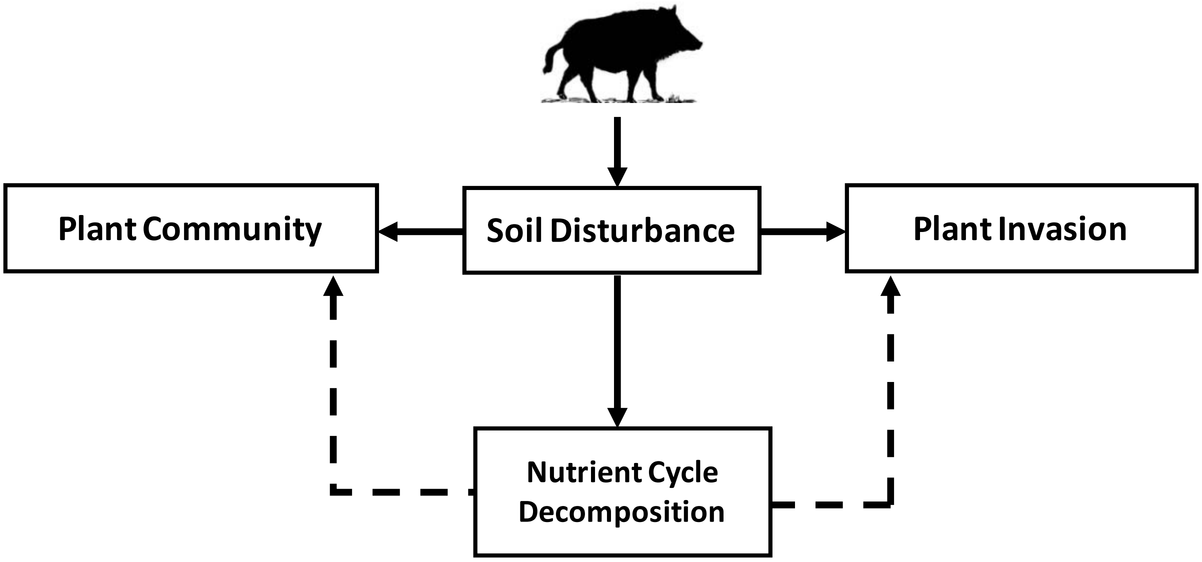

Figure I.1.Wild boar rooting disturbance can directly alter plant communities composition (Chapter III) and physical properties of soils, which in turn may influence ecosystem processes such as nutrient cycling and decomposition rates (Chapter IV). Additionally, rooting disturbance can promote the spread of exotic plants directly by dispersing them or indirectly by enhancing their establishment in rooted patches (Chapter V, solid arrows). The changes in the belowground system can indirectly affect aboveground communities (dashed arrows).

CHAPTER II: IMPACT OF WILD BOAR (*SUS SCROFA*) IN ITS INTRODUCED AND NATIVE RANGE: A REVIEW

The following section is a slightly modified version of a paper published in the journal Biological Invasions:

Barrios-Garcia, M.N and S. Ballari (*in press*) Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. Biological Invasions

As the lead author of this article I was responsible for this paper. My primary contributions to this paper included the literature search, synthesis, and writing.

Abstract

Wild boar are now present on all continents except Antarctica and can greatly affect community structure and ecosystem function. Their destructive feeding habits, primarily rooting disturbance, can reduce plant cover, diversity, and regeneration. Furthermore, predation and habitat destruction by boar can greatly affect animal communities. Effects of wild boar on fungi and aquatic communities are scarcely studied, and soil properties and processes seem more resistant to disturbance. Wild boar also affect humans' economy as they cause crop damage and transmit diseases to livestock and wildlife. In this review, we found that most of the published literature examines boar effects in their introduced range and little is available from the native distribution. Because most of the research describes direct effects of wild boar on plant communities and predation on some animal communities, less is known about indirect effects on ecosystem function. Finally, predictive research and information on ecosystem recovery after wild boar removal are scarce. We identified research gaps and urge the need to lower wild boar densities. Identifying commonalities among wild boar impacts on native ecosystems across its introduced range will help in the design of management strategies.

Keywords: rooting, disturbance, feral pig, wild hog, non-native species.

Introduction

Wild boar (*Sus scrofa*), native to Eurasia, are now present on all continents except Antarctica, and many oceanic islands (Long 2003, Figure II.2), making boar one of the most widely distributed mammals in the world (Massei and Genov 2004). Wild boar are one of the oldest recorded intentional mammal introductions by humans, as early explorers released them for bush meat throughout the world (Courchamp et al. 2003; Long 2003). However, more recent introductions are motivated by commercial hunting (Courchamp et al. 2003, Long 2003).

Part of the success and impact of wild boar introductions is related to the biology of the species. Wild boar are fecund and reproduce vigorously (Wood and Barrett 1979, Coblentz and Baber 1987, Pavlov et al. 1992, Taylor et al. 1998, Rosell et al. 2001); and the wide native distribution of wild boar, Eurasia and North Africa, suggests they are pre-adapted to a wide range of environmental conditions (Baskin and Danell 2003). Additionally, wild boar have a highly plastic diet, feeding opportunistically on many plants and animals, which can vary greatly by geographic location or season (Stegeman 1938, Genov 1981, Baubet et al. 2004). Non-human predation of wild boar is limited in the native and introduced range because of low predator abundances, natural predator population declines, or intentional removal of predators by humans (Tolleson et al. 1995, Ickes 2001, Massei and Genov 2004). Furthermore, introduced boar populations are aided through illegal stocking by hunters (Wood and Barrett 1979, Spencer and Hampton 2005) and expansion of agriculture (O'Brien 1987), which promote the spread of their populations in nearly every region where they have been introduced

Although wild boar have been studied in great detail in some of the native and introduced ranges (Table II.1; Western Europe: Schley and Roper 2003, Massei and Genov 2004; Australia: Hone 2002; USA: Singer 1981, Campbell and Long 2009, Nogueira-Filho et al. 2009), gaps remain in the knowledge of their effects not only in other locations but also in the understanding of how they alter ecosystem processes and functions. Here we review and synthesize the literature on wild boar effects in their native and introduced ranges, and we identify knowledge gaps and research needs. It should be noted that we used literature on wild boar in the introduced ranges where the feral populations resulted from crossings with domestic pigs. Therefore, some characters might differ between the native and introduced populations.

Negative effects

To feed on belowground plant parts, fungi, and invertebrates, wild boar overturn extensive areas of soil vegetation (Baubet et al. 2003, Cushman et al. 2004). This habit not only directly affects above- and belowground components of the communities but also indirectly affects other organisms by physically changing habitat characteristics and modifying resource availability (Jones et al. 1994, 1997, Vitousek et al. 1997, Crooks 2002). Because the rooting behavior has marked ecosystem-level effects, wild boar are considered ecosystem engineers (Vitousek 1990, Jones et al. 1994, Crooks 2002, Hone 2002). Variation in rooting occurrence is reported among communities and vegetation types (Howe and Bratton 1976, Baron 1982, Graves 1984, Coblentz and Baber 1987, Barrett et al. 1988, Mitchell et al. 2007b, Solís-Cámara et al. 2008, Pescador et al. 2009). Nevertheless, some have suggested that rooting can be predicted by environmental factors (e.g. soil moisture, slope, tree density, understory cover; Bratton 1975, Coblentz and Baber 1987, Hone 1988).

Effects on soil properties

Wild boar rooting directly alters soil structure and processes; however, few studies explore the influence of wild boar on soil properties. The rooting disturbance could be comparable to tillage treatment in agroecosystems. The agricultural literature indicates that tillage increases nutrient cycling and decomposition rates, while nutrient loss through leaching is greater in tillage than no tillage (Hendrix et al. 1986). However, the research available on the consequence of rooting on soil processes shows contrasting results. In the introduced range, in the Great Smoky Mountains National Park (GSMNP), USA, Singer et al. (1984) found that rooting disturbance thoroughly mixed and reduced the depth of the upper soil horizons (i.e., layers O1, O2, A1, and A2) and decreased bulk density, although with no significant effects in sediment yield. Relative to undisturbed areas, disturbed soils had lower Ca, P, Mg, Mn, Zn, Cu, H, and N concentrations and cation exchange capacity (Singer et al. 1984). However, NO_3-N and NH_4-N were greater in rooted soil, indicating boar activity altered N-transformation processes (Singer et al. 1984). Similarly, Siemann et al. (2009) found that rooted plots in pine-hardwood forest in the USA had accelerated nitrogen mineralization rates and consequently lower C:N ratios. In contrast, Cushman et al. (2004), Tierney and Cushman (2006), and Moody and Jones (2000) found no evidence that wild boar rooting disturbance affected soil texture, pH, moisture, organic matter, or nitrogen mineralization rates in grasslands and oak woodlands of California. Likewise, Mitchell et al. (2007a) found no significant effects of wild boar digging on litter biomass or soil moisture in Australian rainforest. To date no measurements of wild boar disturbance on decomposition rates or microbial activity are available. Alternatively, it could be suggested that rooting disturbance effects will vary with plant communities (e.g., grasslands vs. forests) and time since disturbance as changes might fade as time proceeds. However, the limited number of studies across communities (1 rainforest, 1 evergreen forest, 2 deciduous forests and 1 grasslands) and the lack of measurements across time (but see Tierney and Cushman 2006) preclude this analysis.

In the native range, data are also scarce and inconsistent. Groot Bruinderink and Hazebroek (1996) found no effect of rooting on soil horizon depths, soil pH, organic matter, and NO_3-N and NH_4-N contents in the Netherlands. Morh et al. (2005) simulated soil disturbance by wild boar and obtained similar results in Germany. However, they found that artificial disturbance decreased potassium and magnesium content and microbial activity. The reduction of microbial activity could result from direct disturbance of soil structure and microclimate or indirect reduction of saprophagous arthropod abundance (Mohr et al. 2005). However, to date there are no studies on the cascading effect that soil fauna predation might have on soil processes. Furthermore, Risch et al. (2010) in Switzerland found no effect of rooting on soil temperature, but a significant increase in soil respiration and microbial and fine root biomass, and a decrease in soil moisture. Nevertheless, the effects of rooting on microbial and fine root biomass disappeared two years after the initial rooting event, suggesting that soils recover to their pre-rooting condition (Risch et al. 2010). Lastly, Wirthner et al. (2011) found no significant effect of rooting on microbial biomass carbon or soil bacterial community structure, diversity, richness and evenness. The absence of studies in other locations and idiosyncratic results of the few studies available prevent general agreement on wild boar effects on soil properties.

Effects on plant communities

The most obvious direct effect of rooting by wild boar is the reduction in plant cover. In the introduced range, the extent of rooting varies depending on the season (Baron 1982, Sierra 2001), but this activity can reduce as much as 80% of understory cover (Singer et al. 1984). Although wild boar are omnivorous, plant matter comprises the majority of their diet (Everitt and Alaniz 1980, Chimera et al. 1995, Adkins and Harveson 2006, Cuevas et al. 2010). The consequences of this activity vary with plant community, but generally rooting decreases species diversity (Bratton 1975, Kotanen 1995, Hone 2002, Tierney and Cushman 2006, Siemann et al. 2009) and regeneration (Challies 1975, Lipscomb 1989, Drake and Pratt 2001, Sweitzer and Van Vuren 2002, Mitchell et al. 2007a, Desbiez et al. 2009, Siemann et al. 2009, Busby et al. 2010, Webber et al. 2010) and alters species composition (Bratton 1974, Siemann et al. 2009), which could lead to local extirpation of species (Recher and Clark 1974, Challies 1975, Singer et al. 1984).

While rooting, wild boar dig up plants of several species; however, damage may affect specific species (Bratton 1974, Challies 1975, Wood and Barrett 1979, Everitt and Alaniz 1980, Baron 1982, Graves 1984, Stone 1985, Coblentz and Baber 1987, Loope et al. 1988, Hone 2002) or be greater on species with fleshy roots or corms (Bratton 1974, Howe and Bratton 1976, Howe et al. 1981, Graves 1984, Dardaillon 1986, Barrett et al. 1988, Pavlov et al. 1992, Chimera et al. 1995, Jaksic 1998, Adkins and Harveson 2006, Skewes et al. 2007, Cuevas et al. 2010). The consequences for plant fitness are barely explored, with contrasting results. Lacki and Lancia (1986) argue that disturbance may benefit the growth of some plant species, while Siemann et al. (2009) found that disturbance decreases plant height growth. Mitchell et al. (2007a) reported the only records on the effects of rooting on seedling survival and plant biomass in Australian rainforests, where rooting decreased seedling survival but had no effect on plant biomass. Further, nothing is known about the effect of rooting on other plant fitness traits such as flower production and seed set.

Some plant communities are more resilient to disturbance by wild boar. Baron (1982) found that in areas where the vegetation is adapted to frequent disturbances, the original plant cover recovers within 6 month to a year after disturbance. Similarly, Kotanen (1995) observed that species richness in California coastal prairie returned to undisturbed control levels within a year following rooting disturbance. Predicting where rooting is likely to occur and the effects it might have appears contingent on the biology and disturbance history of the affected plant community; however, forecasting damage would aid the design of management strategies.

One of the main concerns about rooting is the fact that soil disturbance by wild boar is associated with increased abundance of exotic plant taxa. Although rooting creates a mosaic of disturbed and undisturbed vegetation patches that constitute safe sites for colonization by both native and exotic plants, many studies have reported an increase of exotic abundance (Singer et al. 1984, Stone 1985, Loope et al. 1988, Aplet et al. 1991, Pavlov et al. 1992, Cushman et al. 2004, Tierney and Cushman 2006, Siemann et al. 2009). It is unknown, however, whether exotic plant community composition is the cause or an effect of rooting disturbance. The increased abundance of exotic species may result from localized soil disturbance, or alternatively wild boar may be drawn to areas with higher abundances of exotic species (Aplet et al. 1991). Research on the mechanism behind this pattern is rare. Changes in light availability, nutrient availability, or seed dispersal are some of the possible explanations, but only some of these variables have been tested in isolation, so no general conclusion can be reached.

Another aspect of wild boar behavior that may alter plant community composition is fruit and seed consumption (endozoochory), which may subsequently lead to mortality of the seed. In the introduced range, fruit consumption by wild boar has been documented mainly through the presence of fruit in stomach contents (Wood and Barrett 1979, Everitt and Alaniz 1980, Diong 1982, Stone 1985, Coblentz and Baber 1987, Pavlov et al. 1992, Taylor and Hellgren 1997, Solís-Cámara et al. 2008, Desbiez et al. 2009), but information on seed dispersal is scarce. Grice (1996) and Lynes and Campbell (Lynes and Campbell 2000) found that wild boar in Australia disperse seed of the exotic plant species *Prosopis pallida, Cryptostegia grandiflora* and *Ziziphus mauritiana*. However, research conducted in other introduced ranges showed that wild boar act as seed predators, damaging most if not all of the seeds consumed (Rudge 1976, Lott et al. 1995, Campos and Ojeda 1997, Gomez et al. 2003, Sanguinetti and Kitzberger 2010). Similar conclusions were drawn by Siemann et al. (2009), as they found that seedlings with large seed mass were twice as abundant in fenced plots as in controls. Epizoochory (the dispersal of seeds attached to the animal’s fur) has not been studied in the introduced range and, together with endozoochory, might be key in explaining the association between rooting disturbance and exotic plant species presence. In the native range, wild boar diet consists of ~ 90% plant matter (Genov 1981, Fournier-Chambrillon et al. 1995, Baubet et al. 2004, Herrero et al. 2004, Giménez-Anaya et al. 2008), and boar also prefer specific plant species (Dardaillon 1986, Herrero et al. 2004) as well as specific plant parts, such as bulbs (Dardaillon 1986, Baubet et al. 2004). Rooting frequency seems to vary by plant community type (Dardaillon 1986, Groot Bruinderink and Hazebroek 1996, Welander 2001), and some authors detect seasonal variation (Genov 1981, Dardaillon 1986, Abaigar et al. 1994, Focardi et al. 2000, Welander 2001), though others do not (Groot Bruinderink and Hazebroek 1996). In the Netherlands, rooting also negatively affected regeneration of some native species, but no differences were detected for other species (Groot Bruinderink and Hazebroek 1996). In Malaysia, wild boar reduced tree recruitment, stem density, and species richness in an exclosure experiment (Ickes et al. 2001). Ickes et al (2001) also found that rooting reduced plant growth by 50 percent in trees between 1-7 m tall; however, they found no effect on smaller trees, or on tree mortality in any size class. Studies comparing the effect of wild boar rooting on plant communities in the native and introduced range as well as more information from the native range will help to assess if wild boar impacts differ among ranges and if native plant communities are more resilient to boar disturbance.

Depending on the season, in the native range fruits can comprise up to 60-90% of boar stomach content (Fournier-Chambrillon et al. 1995, Irizar et al. 2004, Herrero et al. 2005). Acorns are the main target, but as in the introduced range little is known concerning the fate of ingested seeds. In Germany, endozoochory and epizoochory of native and exotic species were documented for boar, but the number of viable seeds in the feces was the lowest compared to feces of three other native mammals, while epizoochory had a greater role in long distance dispersal than did dispersal by roe deer (Heinken et al. 2002, Heinken and Raudnitschka 2002, Schmidt et al. 2004). Dispersal by wild boar is an important mechanism for native species such as *Juncus effusus*, *Urtica dioca* and *Betula pendula* (Heinken and Raudnitschka 2002, Schmidt et al. 2004) as well as for exotics such as *Poa pratensis* (Heinken and Raudnitschka 2002, Schmidt et al. 2004)

Effects on animal communities

In their introduced range, predation, nest and habitat destruction, and resource competition with other animals are the primary ways wild boar can affect native animal communities (Long 2003, Cruz et al. 2005), but predation is most often documented. Depending on the ecosystem and the season, animal matter can constitute up to ~30% of wild boar diet (Challies 1975, Baron 1982, Diong 1982, Chimera et al. 1995). Wilcox and Van Vuren (2009) hypothesized that protein deficiency in the summer and fall might be an important factor influencing animal predation rates. Nevertheless, wild boar seem to prey on anything without much preference. They are reported to prey on soil meso- and macrofauna, reducing their abundances between 40-90% (Howe et al. 1981, Singer et al. 1984, Pavlov and Edwards 1995). Species consumed include insect larvae, beetles, snails, centipedes, and earthworms (Stegeman 1938, Recher and Clark 1974, Challies 1975, Everitt and Alaniz 1980, Wood and Roark 1980, Howe et al. 1981, Baron 1982, Diong 1982, Graves 1984, Singer et al. 1984, Coblentz and Baber 1987, Pavlov et al. 1992, Pavlov and Edwards 1995, Tolleson et al. 1995, Taylor and Hellgren 1997, Coleman et al. 2001, Sierra 2001, Skewes et al. 2007, Solís-Cámara et al. 2008, Desbiez et al. 2009). Predation also affects all vertebrates: amphibians, reptiles, mammals, and birds and it is mostly documented by the presence of animal remains in stomach contents (Stegeman 1938, MacFarland et al. 1974, Challies 1975, Rudge 1976, Wood and Roark 1980, Howe et al. 1981, Coblentz and Baber 1987, Cruz and Cruz 1987, Pavlov and Edwards 1995, Tolleson et al. 1995, Taylor and Hellgren 1997, Rollins and

Carroll 2001, Saniga 2002, Schaefer 2004, Fordham et al. 2006, Means and Travis 2007, Wilcox and Van Vuren 2009, Jolley et al. 2010). Furthermore, egg predation can be critical for endangered populations of reptiles such as tortoises (Fordham et al. 2006), iguanas (Wood and Barrett 1979), caimans (Campos 1993), and ground-nesting birds including quail and penguins (Stegeman 1938, Challies 1975, Coblentz and Baber 1987, Pavlov et al. 1992, Tolleson et al. 1995, Desbiez et al. 2009).

Compared to predation, habitat degradation and nest destruction are less explored. To date, we know that feeding by wild boar can destroy habitat for tunneling and ground-dwelling animals, such as frogs, salamanders, voles, chipmunks, and birds (Stegeman 1938, Recher and Clark 1974, Singer et al. 1984, van Riper III and Scott 2001, Means and Travis 2007, Jolley et al. 2010). Furthermore, trampling increases soil compaction, which adversely affect microarthropod communities. The only study conducted on this subject shows that litter-dwelling animals increased tenfold in recovered forest areas (in exclosures), with springtails (Collembola) the most responsive group (Vtorov 1993). Even though soil microarthropods are important components of soil formation processes, little is known about the effect of wild boar on them.

Most resource competition studies focus on native counterparts of boar, e.g. peccaries (*Tayassu tajacu*), but competition is suggested for other species. For peccaries, some argue that their niche does not overlap that of boar (Desbiez et al. 2009), while others demur (Ilse and Hellgren 1995, Gabor and Hellgren 2000, Sicuro and Oliveira 2002). Gabor and Hellgren (2000) found the peccary population in sites lacking boar had 5–8-fold higher densities, suggesting competitive displacement. Suggested competition, due to diet overlap, has been reported with cassowaries in Australia (Crome and Moore 1990), deer in the US and Argentina (Stegeman 1938, Wood and Barrett 1979, Everitt and Alaniz 1980, Wood and Roark 1980, Graves 1984, Taylor and Hellgren 1997, Pérez Carusi et al. 2009), raccoon and opossum in Tennessee (Stegeman 1938), turkey in the US (Wood and Barrett 1979, Graves 1984), squirrels and black bear in the US (Wood and Barrett 1979), cranes in the US (Everitt and Alaniz 1980), and terrestrial vertebrates in California, US (Sweitzer and Van Vuren 2002).

In their native range, wild boar also feed on species from all animal groups: invertebrates (Genov 1981, Fournier-Chambrillon et al. 1995, Baubet et al. 2003, Schley and Roper 2003, Baubet et al. 2004, Herrero et al. 2004, Irizar et al. 2004, Herrero et al. 2005, Mohr et al. 2005, Herrero et al. 2006, Giménez-Anaya et al. 2008), amphibians and reptiles (Genov 1981, Schley and Roper 2003, Irizar et al. 2004, Herrero et al. 2006), mammals (Genov 1981, Schley and Roper 2003, Irizar et al. 2004, Herrero et al. 2005, Herrero et al. 2006, Giménez-Anaya et al. 2008), and birds (Genov 1981, Schley and Roper 2003, Herrero et al. 2004, Herrero et al. 2006, Giménez-Anaya et al. 2008). Additionally, nest predation was recorded in wetlands in Spain (Giménez-Anaya et al. 2008). Although animals are a minor component of wild boar diet (<10% of stomach content) (Genov 1981, Fournier-Chambrillon et al. 1995, Baubet et al. 2004, Irizar et al. 2004), they are consumed throughout the year, suggesting they are an essential food item (Genov 1981, Fournier-Chambrillon et al. 1995, Rosell et al. 2001). Other wild boar consequences, such as habitat and nest destruction and competition with animal communities in their native range have been largely unexplored. The only research conducted on competition with small mammals was in Italy, where wild boar actively searched for buried acorns (Focardi et al. 2000).

Another threat to native animals imposed by wild boar is hybridization. In Java, hybridization between *S. verrucosus*, an endemic species, and wild boar has been documented. While the exact implications of these hybrids are unknown, they pose a potentially serious threat to the survival of *S. verrucosus* (Blouch and Groves 1990). Similarly, in Africa there is some evidence of hybridization between wild boar and the

African bushpig (*Potamochoerus porcus*) (Long 2003). Another example of this phenomenon occurs in New Guinea, where wild boar populations in Ceran and some of the smaller islands in the Molucca appear to be hybrids between introduced stocks of *S. scrofa* and the native *S. celebencis* (Long 2003).

Effects on fungi

Although fungi are reported as part of wild boar diet in the introduced (Wood and Roark 1980, Baron 1982, Skewes et al. 2007) and native ranges (Genov 1981, Genard et al. 1988, Fournier-Chambrillon et al. 1995, Baubet et al. 2004, Herrero et al. 2004, Herrero et al. 2005), little is known about overall effects on fungus populations. Wild boar are trained to detect truffles, as they have an excellent sense of smell. However, the role of wild boar as fungivores has rarely been documented. According to Skewes et al. (2007), fungi occur in wild boar diets more frequently in the introduced range (~60%) than in the native range (~30%), but this proportion varies seasonally in both ranges (Wood and Roark 1980, Genov 1981, Fournier-Chambrillon et al. 1995, Baubet et al. 2004). Genard et al. (1988) hypothesized that wild boar might disseminate hypogeous fungal spores necessary for forest regeneration and that this activity may favor the genetic mixing of spatially separated fungus populations.

Effects on aquatic communities

Relative to the amount of research available on wild boar impacts on terrestrial communities, their effect on aquatic communities has received little attention. Rooting by wild boar may affect aquatic communities similarly to terrestrial communities, by altering aquatic plant and animal community composition, changing water quality and chemistry, and dispersing plants, animals, and diseases or pathogens to isolated systems. In the introduced range, wild boar are reported to decrease macrophyte cover in lagoons (Doupé et al. 2010) and marshes (Arrington et al. 1999) but increase plant species richness (Arrington et al. 1999). Wild boar diet includes seaweed (Challies 1975, Chimera et al. 1995), aquatic plants (Everitt and Alaniz 1980), and aquatic invertebrates, such as clams, mussels, and crayfish (Wood and Roark 1980, Fordham et al. 2006). Doupé et al. (2010) found no effect on fish and macroinvertebrate composition when comparing fenced and unfenced lagoons. In streams in the USA, Kaller and Kelso (2006) reported a negative effect of wild boar on collecting and scraping aquatic insects and an increased abundance of stream pathogens and gastropods. Finally, there is evidence that wild boar promote invasion by dispersing a woody weed invading wetlands in Australia (Setter et al. 2002).

Wild boar activity has been found to alter water quality and chemistry, although the direction of the changes varies among sites. In the USA, Singer et al. (1984) reported nitrate content doubled in rooted streams, and in Australia, Doupé et al. (2010) found higher turbidity, anoxic conditions, and enhanced acidity in lagoons. Furthermore, Doupé et al. (2010) found no effect on nutrient content (i.e., N and P). Similarly, a study in a Hawaiian watershed showed that only total suspended solids increased in response to wild boar activity but that the amount of runoff, total dissolved solids, and nutrient content did not change (Browning 2008). In contrast, Dunkell et al. (2011) found that rooting by wild boar in Hawaii decreased runoff but had no effect on total suspended solids.

In the native range boar use marshes throughout the year (Dardaillon 1986), feed on *Juncus*, crab, fish, amphibians, and birds (Genov 1981, Herrero et al. 2004, Herrero et al. 2006, Giménez-Anaya et al. 2008), and can disperse freshwater invertebrate taxa including rotifers, cladocerans, copepods, and ostracods (Vanschoenwinkel et al. 2008).Unfortunately, no data are available from the native range on the effect of wild boar on water chemistry, and to date there are no records of the consequences of changes in water chemistry on the associated animal and plant communities, both in the introduced and native ranges.

Other disturbances

While rooting behavior by boar has the widest range of community impacts, wallowing, rubbing trees, and nest building can also be important. Wallowing provides boar protection from insects and parasites and assists with thermoregulation (Graves 1984, Heinken et al. 2006, Campbell and Long 2009). After wallowing, the animal will find a tree to rub against, which is suspected to remove parasites (Graves 1984, Campbell and Long 2009) or potentially to be simply a comfort behavior (Graves 1984). Nest-building occurs prior to giving birth when female boar harvest vegetation to build a mound under which they deliver their young (Ickes et al. 2001). Most of the literature available on the effect of these behaviors comes from the native range. Wallows are typically found in moist sites, such as edges of flooded areas, muddy beds of canals or marshes (Dardaillon 1986), and rubbing trees are generally located very close to wallows (Dardaillon 1986, Heinken et al. 2006, Campbell and Long 2009). Boar might show a preference for tree species to rub on, but evidence is limited (Dardaillon 1986). Both wallowing and rubbing trees have been found as important passive dispersal vectors of invertebrates and seeds (Heinken et al. 2006, Vanschoenwinkel et al. 2008), even for plant species with no features favoring this type of dispersal (Heinken et al. 2006). Boar prefer nest areas with abundant plant cover that are near water (Dardaillon 1986, Fernández-Llario 2004) and could cause substantial changes in tree community composition (Ickes et al. 2003, Ickes et al. 2005). Wild boar in the Malaysian rain forest snap or uproot an average of 267 woody saplings to build a single nest (Ickes et al. 2005). This behavior affects on average 244 m^2 of understory area and causes an estimated 29% of the observed tree mortality of saplings 1–2 cm dbh, (Ickes et al. 2005).

The only records of wallowing and tree rubbing in the introduced range are in the southeastern USA and New Zealand (Stegeman 1938, McIlroy 1989). Wild boar wallows were found near the upper ends of the higher cove forests, in shaded, cool, and wet places, and creek beds (Stegeman 1938, McIlroy 1989). The wallowing habit was continuous throughout the year in the USA (Stegeman 1938) and more seasonal in New Zealand (McIlroy 1989). As in the native range, wallowing was closely associated with rubbing (Stegeman 1938, McIlroy 1989). Interestingly, in the USA there was a clear preference for *Pinus rigida* for rubbing, although nothing is known about the effect rubbing might have on the species (Stegeman 1938, Graves 1984). Future research should evaluate wallowing and rubbing behavior further and nest-building in other areas of the introduced range.

Another feature of wild boar that has received little attention is the consequence of wild boar wastes. These are very conspicuous in places such as in Hawaii, where nutrient limitation is an important influence on plant community composition. Cuddihy and Stone (1990) reported that wild boar activities increased N influx and diminished the adaptive advantage of native species over exotics. However, this hypothesis is untested.

Economic consequences: crop and husbandry damage

Wild boar can damage crops and husbandry, causing significant economic losses. In the USA alone, wild boar crop damage cost is estimated to be $800 million/year (Pimentel et al. 2005). In the introduced range wild boar feed and root on different crops such as cereal, sorghum, maize (Kilham 1982, Caley 1993), pasture (Desbiez et al. 2009), and pine plantations (Wood and Barrett 1979, Lipscomb 1989). According to Mayer et al. (2000), the most widespread and costliest forest damage by wild boar is depredation of planted pine seedlings, primarily longleaf pine (*Pinus palustris*), slash pine (*P. elliotti*), loblolly pine (*P. taeda*), and pitch pine (*P. rigida*). Predation by wild boar has also been found to reduce production and harvest of lambs (Pavlov et al. 1981, Pavlov and Hone 1982) and turtles (Fordham et al. 2006).

Boar damage of crops seems to be worse in the native range, where 37 - 88% of a wild boar’s diet is agricultural plants (Genov 1981, Fournier-Chambrillon et al. 1995, Herrero et al. 2004, Herrero et al. 2006, Giménez-Anaya et al. 2008). The most affected crop is maize (corn), but acorns, beechnuts, chestnuts, pine seeds, olives, cereal grains, sunflower seeds, wheat, barley, alfalfa, oil palm trees fruit, sugarcane, grapes, and potatoes are also damaged (Genov 1981, Dardaillon 1986, Fournier-Chambrillon et al. 1995, Ickes 2001, Schley and Roper 2003, Calenge et al. 2004, Herrero et al. 2004, Herrero et al. 2006, Giménez-Anaya et al. 2008). Crops provide an extremely rich food source with minimal foraging effort (Caley 1993); indeed, Wilson (2004) found damage mainly occurred in fields adjacent to woodlands. Furthermore**,** crop residues (stubble) left after harvesting provide a continuing food source that wild boar exploit (Caley 1993). Supplementary feeding is suggested as a way to mitigate crop and vineyard damage (Andrzejewski and Jezierski 1978, Calenge et al. 2004), but some studies show no effects of supplementation on crop damage or when comparing stomach contents (Groot Bruinderink et al. 1994, Geisser and Reyer 2004). However, it seems that natural resources are sometimes preferred over cultivated plants. For example, Mackin (1970) and Genov (1981) found that crop damage decreased when acorn crops were high.

Hybridization with domestic pigs may have economic consequences in the native and introduced ranges (Waithman et al. 1999, Koutsogiannouli et al. 2010). However, little is known about the effect of hybrids on meat production or populations of free-ranging hybrids.

Transmission of diseases and zoonoses

Wild boar are reservoirs of a number of viral and bacterial diseases as well as parasites (Rosell et al. 2001, Baubet et al. 2003, de la Fuente et al. 2004, Gortázar et al. 2007, Ruiz-Fons et al. 2008). Many of these diseases and parasites pose a risk to humans, livestock, and wildlife and can be transmitted by direct contact with wild boar or their feces, or by eating contaminated food or uncooked boar meat. Boar-borne diseases have economic costs including livestock mortality, disease control, and eradication programs (Gee 1982, Pavlov et al. 1992, Gortázar et al. 2007, Ruiz-Fons et al. 2008).

Some diseases of great concern for human health include brucellosis, leptospirosis, *Escherichia coli* (Browning 2008), trichinellosis (Pavlov et al. 1992, Pavlov and Edwards 1995), tuberculosis (Gortázar et al. 2007), toxoplasmosis (Antolova et al. 2007), Japanese encephalitis virus (Bradshaw et al. 2007), and tick-borne diseases (de la Fuente et al. 2004). Diseases that affect livestock and wildlife include brucellosis, tuberculosis (Gortázar et al. 2007), classical swine fever (Wood and Barrett 1979), porcine parvovirus (Ruiz et al. 2009), Aujeszky´s disease virus -pseudorabies- (Murray and Snowdon 1976, Höfle et al. 2004), triquinellosis (Gortázar et al. 2007), African swine fever, swine erysipelas (Risco et al. 2011), salmonellosis (Vengust et al. 2006), and foot and mouth disease (Murray and Snowdon 1976, Gee 1982). Other diseases that can be carried and transmitted to domestic animals include swine fever, swine influenza, vesicular stomatitis, vesicular exanthema, and swine vesicular disease (Pavlov et al. 1992).

There is much speculation about the potential danger posed by wild boar as carriers and transmitters of disease to native wildlife, but little is known about the consequence of disease transmission by wild boar. The only exception is bovine tuberculosis, which was found to be transmitted from wild boar to brushtail possums (*Trichosurus vulpecula*) in New Zealand. In the native range, in Spain, bovine tuberculosis is present in wild boar, red deer (*Cervus elaphus*), and Iberian lynx (*Lynx pardina*), indicating a common source of infection (Briones et al. 2000).

Lastly, wild boar are implicated in the spread of dieback disease (*Phytophthora cinnamomi*). Li et al. (2010) show that *Phytophthora cinnamomi* spores can survive passage through the gut, while Kliejunas and Ko (1976) recovered spores from soil particles from boar hoofs in Hawaii.

Indirect effects and unexpected interactions

Wild boar are involved in complex interactions with direct and indirect effects on the biological and physical components of the environment. However, information from both the introduced and native ranges on indirect effects is scarce.

In the introduced range, wild boar may indirectly affect bird communities by reducing the availability of food resources. For example, in Hawaii the foraging behavior of boar negatively affect native birds by reducing the abundance and amount of nectar produced by understory plants, such as *Rubus hawaiiensis* (Stone 1985). Also, wild boar can alter native species interaction dynamics. In the USA, Henry (1969), found reduced egg predation by snakes in areas where wild boar were present. Wild boar may drive off or prey on native predators, especially snakes, and thus decrease native predator populations. However, wild boar seem to replace native predators, given that total predation is neither reduced nor increased. This may explain why turkey and grouse maintain populations in areas where wild boar have been introduced (Henry 1969). Additionally, wild boar may indirectly affect disease transmission. Lease et al. (1996) found correlations between wild boar activity and the abundance and distribution of mosquitoes (*Culex sp*.), which are vectors of diseases such as avian pox and malaria. Boar rooting activity creates new breeding habitats for mosquito larvae, which can increase their abundance. These diseases have devastating effects on the endemic Hawaiian avifauna (Warner 1968).

Furthermore, boar may be involved in invasional meltdown in Hawaii, where presence of an exotic earthworm, *Pontoscolex corethurus*, provides extra animal protein increasing boar populations to extreme levels (Diong 1982). Additionally, Diong (1982) reported that exotic earthworms aggregate under wild boar wastes where nutrient availability is higher. However, to date, no one has studied this interaction. Finally, in their introduced range wild boar alter the structure of food webs. For example, in the California Channel Islands (USA) Roemer et al. (2002) showed a unique multiple interaction between three native species and wild boar. Abundant wild boar subsidized the golden eagle (*Aquila chrysaetos*) population, which drove the island fox (*Urocyon littoralis*) to near extinction through hyperpredation, and indirectly caused an increase in island skunks (*Spilogale gracilis*) by means of competitive release. This example highlights that future research should consider indirect interactions of wild boar, as this type of interaction could have unpredictable consequences.

On the other hand, the only record of indirect effects of wild boar within the native range involves dispersal facilitation. In France, wild boar ingest earthworms and dung beetles infested by lung and stomach nematodes, contributing to the dispersal of these parasites (Humbert and Henry 1989).

Positive effects

Although most research on wild boar in their introduced range reports negative effects on native ecosystems, some positive aspects of boar introduction should be acknowledged. In some cases wild boar are prey items for native animals, such as Florida panthers (*Puma concolor*), bobcat (*Lynx rufus*), and dingoes (*Canis familiaris*) (Stegeman 1938, Woodall 1983, Maehr et al. 1990). In addition, Kilham (1982) and Baber and Morris (1980) reported cleaning-feeding symbioses with birds, in which the Florida scrub jay (*Aphelocoma coerulescens*) and common crow (*Corvus brachyrhynchos)* have been observed to forage on wild boar ectoparasites.

Rooting disturbance by wild boar can be a substitute for natural disturbances. For example, Kotanen (1995) suggested that boar can help maintain the native component of species richness by creating habitat for native species, replacing the effects of natural wildfires, which are effectively suppressed in several areas. Everitt and Alaniz (1980) suggest rooting is beneficial to native wildlife because early-successional plants are found in rooted sites and provide food for wildlife that feed on these species. Similarly, it has been argued that wild boar are the ecological equivalent of the regionally extinct grizzly bear (*Ursus arctos*) in California, USA, where some intermediate level of acorn foraging and rooting disturbance may replace the activities of grizzly bears in oak woodland ecosystems (Sweitzer and Van Vuren 2002). Moreover, Arrington (1999) found that wild boar rooting can increase plant-defined microhabitat diversity.

In the neotropics, wild boar contribute to the preservation of native wildlife. Native species such as peccaries (*Tayassu sp.*), deer (*Mazama sp.*), tapir (*Tapirus terrestris*), and capybara (*Hydrochaeris hydrochaeri*) are hunted and are an important source of animal protein or economic income (Desbiez 2007). However, in the Brazilian Pantanal wild boar are acting as a replacement hunting target, releasing native wildlife from over-harvesting (Desbiez 2007). Wild boar are also appreciated as an economic resource, for both recreational hunting and meat production. In the USA, wild boar hunting has surpassed deer hunting in popularity (Tolleson et al. 1995), with more than 75,000 individuals harvested in one year in Florida alone (Wood and Barrett 1979). Furthermore, as chronic wasting disease is spreading in deer, wild boar hunting is likely to increase in popularity. In Australia, commercialization of wild boar meat provides significant income for depressed rural communities (O'Brien 1987). However, a negative aspect of boar hunting is the creation of incentives to maintain, rather than eradicate, the population (O'Brien 1987, Zivin et al. 2000).

Eradication

Owing to their general biology, reproduction, and behavior, wild boar eradication and management present an extreme challenge. Morrison et al. (2007) indicate that wild boar rapidly recover from population reduction. Furthermore, through selection, conditioning, and/or learning, wild boar that survive early phases of eradication campaigns become more difficult to find (Morrison et al. 2007). Successful eradication examples have taken place on islands where potential for recolonization is low, or in small areas where wild boar-proof fences have been erected (Choquenot et al. 1996). Examples include: Santiago Island - Galapagos, Ecuador (Cruz et al. 2005), Santa Cruz Island - Galapagos, Ecuador (Parkes et al. 2010), fenced preserves of Hawaii, USA (Barron et al. 2011), Annadel State Park - California, USA (Barrett et al. 1988), Santa Catalina – California, USA (Schuyler et al. 2002), Pinnacles National Monument - California, USA (McCann and Garcelon 2008), Santa Rosa Island – USA (Lombardo and Faulkner 1999). Ambitious, but largely unsuccessful reduction programs were conducted across the USA in Great Smoky Mountains National Park, Hawaii Volcanoes National Park, Haleakala National Park, and Canaveral National Seashore (Singer 1981). Based on estimated population sizes in these areas, management programs probably harvested less than 10 percent of the population, or far below the annual increment (Singer 1981).

There are many techniques for management, control, and eradication of wild boar. These include hunting and harvesting, aerial baiting and shooting, snaring, poisoning, trapping, the judas pig technique, and fencing (Barrett et al. 1988, McIlroy 1989, Wilcox et al. 2004, Cruz et al. 2005, McCann and Garcelon 2008, Vidrih and Trdan 2008, Braga et al. 2010, Parkes et al. 2010). Local environmental factors and program duration are important determinants of the success of the campaigns (McCann and Garcelon 2008). It is difficult to compare techniques directly between programs, as some aim for control and others for eradication (McCann and Garcelon 2008).

Eradication of wild boar is possible and has been demonstrated in many parts of the world. However, eradication requires logistically complex and economically intense efforts. In many cases, eradication occurs only with a combination of two or more techniques (Geisser and Reyer 2004, Cruz et al. 2005, McCann and Garcelon 2008). Afterwards, strict control efforts are necessary to prevent future recolonization or reintroduction, and monitoring is needed to assess ecosystem response to eradication.

Discussion

This review analyzes the current knowledge of the impact of wild boar in their introduced and native ranges. Direct effects of wild boar on plant and animal communities are most commonly reported and identified. Overall, wild boar alter plant communities by decreasing plant cover, diversity, and regeneration, whereas animal communities are affected by predation and habitat destruction. Effects of wild boar on fungi and aquatic ecosystems are known to occur, but little is available to allow a general conclusion. Soil properties and processes seem to be more resistant to rooting disturbance or alternatively it might take longer for soil to show wild boar effects. The research available shows that wild boar directly influence the physical and biological components of an ecosystem, demonstrating their role as ecosystem engineers.

Research needs

Although wild boar have been studied for several decades worldwide, we have identified many gaps in information where research is needed. Surprisingly, we found limited information on wild boar effects in their native range, and most was related to crop damage. Limited knowledge of effects on natural native systems made it particularly complicated to compare effects between both ranges (Hierro et al. 2005). It seems that some impacts might differ among ranges - e.g. fungus consumption is greater in introduced ranges than in native ranges (Skewes et al. 2007) However, the scarcity of information from either range prevents us from identifying significant differences among ranges.

Most research in the introduced range has been conducted in the absence of pre-invasion data or by comparing already disturbed and undisturbed areas (Bratton 1974, Cushman et al. 2004, Doupé et al. 2010), making it difficult to accurately determine effects of wild boar on ecosystems. Future research should compare intact or uninvaded areas to those damaged, or alternatively, comparisons of disturbed and undisturbed patches should take place after experiments have been set up in undisturbed areas. Otherwise, it is hard to know if wild boar are the cause or the consequence of certain ecosystem changes, such as changes in plant community composition (Aplet et al. 1991).

Much of the information available is descriptive or anecdotal, and most comes from technical, government, or wildlife reports. For example, analysis of boar stomach contents describes predation on birds, but little is known about the effect on bird populations. Furthermore, the lack of manipulative experiments also reduces the possibility of assessing effects of wild boar on native ecosystems. For example, we know wild boar prey on earthworms but do not know the consequences of decreased earthworm abundance on soil properties and nutrient cycles. Moreover, we found that wild boar create intricate biological relationships, generating multiple interactions with the environment in which all ecosystem components are altered. Therefore, future research should integrate wild boar impacts in a whole-ecosystem approach, where both direct and indirect effects are evaluated.

We found no predictive studies (but see Hone 1995). As researchers have done for other large mammals (e.g. deer, Côté et al. 2004), it would be helpful to identify indicators of ecosystem degradation and use them to define a threshold at which ecosystem functioning is affected. This will allow the prediction of future damage. Furthermore, accurately forecasting wild boar damage will help to design sound management strategies.

Lastly, little is known about ecosystem recovery after wild boar removal or eradication. Vtorov (1993) found that fencing and removal of wild boar can restore soil microarthropod communities in 7 years. Further, Cole et al. (*in press*) found a six-fold increase in plant cover after 16 years of wild boar removal, while Donlan et al. (2007) reported an increase of over an order of magnitude in the density of the endemic Galapagos rail (*Lateranllus spilonotus*) after wild boar eradication on Santiago Island. Finally, Taylor et al. (2011) reported significant increases in seedling density, soil macroinvertebrates, and leaf litter cover, but no effect on soil pH, invertebrate diversity, vegetation diversity, and tree density following wild boar exclusion for 12 years. Knowing if communities will be able to recover and how long it will take is also crucial for the design of management strategies.

Conclusion

Although the effects of wild boar have been studied in several areas where they have been introduced, further research is needed. Given the influence of wild boar on community structure and ecosystem function, it is necessary to assess the consequences of their interaction with native ecosystems and their long-term effects. Understanding how wild boar damage varies across introduced ranges and in comparison to the native range will help with the design and prioritization of management plans. Overall our review clearly shows that wild boar alter all components of ecosystems thus providing strong arguments for wild boar control. In the light of ecosystem recovery after wild boar removal we believe that management plans should aim to lower wild boar densities or when possible to eradicate the populations (e.g. islands or fence preserves).

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Appendix II: Tables and Figures

Table II. 1. Summary of wild boar effects on ecosystems with study area, type of evidence, reported effect and representative references.

Impact			Study area	Type of evidence	Effect	Representative references
Soil						
	Physical properties	Bulk density	Introduced	Descriptive	-	Singer et al. 1984
		Soil texture	Introduced	Experimental	0	Cushman et al. 2004, Tierney and Cushman 2006
		Soil moisture	Introduced	Experimental	0	Moody and Jones 2000, Mitchell et al. 2007a
		pH	Introduced	Experimental	0	Moody and Jones 2000
	Chemical properties	Nutrient content	Introduced	Descriptive/Experimental	0 / + / -	Singer et al. 1984, Moody and Jones 2000
		N mineralization	Introduced	Experimental	+ / 0	Cushman et al. 2004, Siemann et al. 2009
		Soil respiration			?	
	Biological properties	Decomposition			?	
Plant communities		Plant growth	Introduced	Descriptive/Experimental	+ / -	Lacki and Lancia 1986, Siemann et al. 2009
		Survival	Introduced	Experimental	-	Mitchell et al. 2007a
		Reproduction			?	
		Regeneration	Native/Introduced	Descriptive/Experimental	-	Ickes et al. 2001, Sweitzer and Van Vuren 2002
		Plant cover	Introduced	Descriptive/Experimental	-	Singer et al. 1984
		Species diversity	Introduced	Descriptive/Experimental	-	Bratton 1975, Hone 2002
		Seed				
		Predation	Introduced	Experimental	+	Lott et al. 1995, Sanguinetti and Kitzberger 2010
		Dispersal	Native/Introduced	Descriptive	Native &	Lynes and Campbell 2000, Heinken et al. 2002
		endozoochory	Native	Descriptive	invasive sp	Heinken and Raudnitschka 2002
		Dispersal			+ / ?	
		ectozoochory				

Table II.1 Continue

Animal	Predation				
communities	Invertebrates				
	Vertebrates	Introduced	Descriptive	-	Challies 1975, Taylor and Hellgren 1997
	Effects on pop	Introduced	Descriptive	-	Coblentz and Baber 1987, Jolley et al. 2010
	dynamics			?	
	Habitat and nest	Introduced	Descriptive	-	van Riper III and Scott 2001
	destruction	Native/Introduced	Descriptive/Experimental	- / 0 / ?	Focardi et al. 2000, Desbiez et al. 2009
	Competition	Native	Descriptive	-	Blouch and Groves 1990, Long 2003
	Hybridization				
Fungi	Mycophagy	Native/Introduced	Descriptive	occurs	Fournier-Chambrillon et al. 1995
community	Dispersal	Native/Introduced	Descriptive	? / + / -	Genard et al. 1988
Aquatic					
communities	Plant cover	Introduced	Descriptive/Experimental	-	Arrington et al. 1999, Doupé et al. 2010
Plant	Species diversity	Introduced	Descriptive/Experimental	+	Arrington et al. 1999
community	Predation				
	Invertebrates	Introduced	Descriptive/Experimental	+ / - / 0	Kaller and Kelso 2006, Doupé et al. 2010
Animal	Vertebrates	Native/Introduced	Descriptive	-	Genov 1981
community	Dispersal				
	Plants	Native/Introduced	Descriptive/Experimental	Invasive sp.	Setter et al. 2002
	Invertebrates	Native	Descriptive	+	Vanschoenwinkel et al. 2008
	Nutrients	Introduced	Descriptive/Experimental	+ / 0	Browning 2008, Doupé et al. 2010
	Effect on communities			?	
Water quality and chemistry					

Table II.1 Continue

Other impacts	Wallowing			?	
	Rubbing trees	Introduced	Descriptive	-	Stegeman1938, Graves 1984
	Nest building	Native	Descriptive	-	Ickes et al. 2005
	Wastes	Introduced	Speculative	- / ?	Cuddihy and Stone 1990
Economic	Crops	Native/Introduced	Descriptive	-	Genov 1981, Caley, P. 1993, Schley et al. 2003
	Husbandry	Introduced	Descriptive	-	Pavlov and Hone 1982, Fordham et al. 2006
Disease transmission	Livestock	Native/Introduced	Descriptive	Occurs but no information on consequences	Pavlov et al. 1992, de la Fuente et al. 2004
	Wildlife				Wood and Barrett 1979, Gortázar et al. 2007
	Humans				Gee 1982, Briones et al. 2000

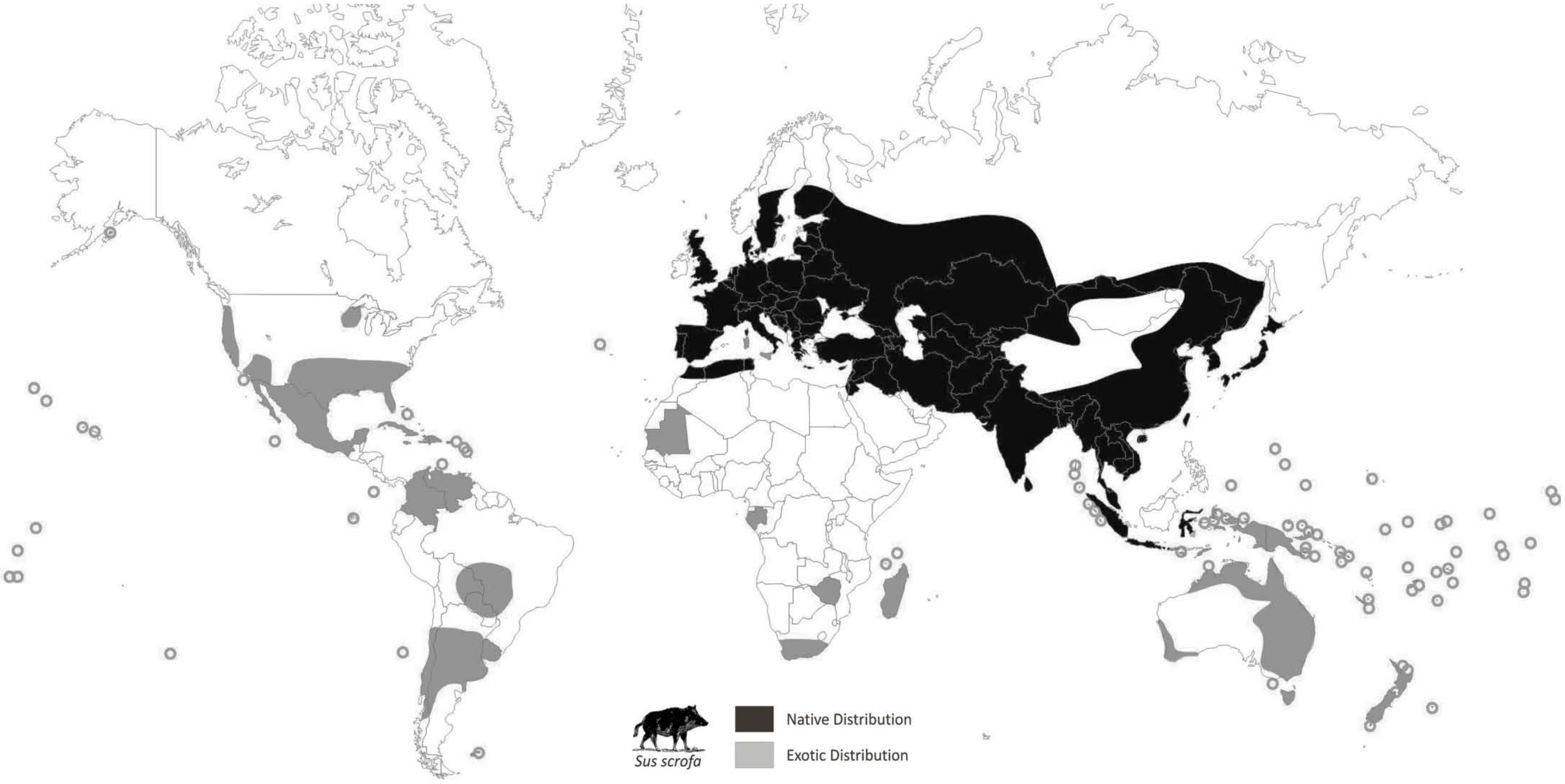

Figure II.2. Worldwide distribution of *Sus Scrofa*. The species native range demarked in black and introduced range in gray. Gray circles indicate the islands where *S. scrofa* have been introduced.

CHAPTER III. INVASIVE HERBIVORES MAY SLOW ECOSYSTEM FUNCTION OVER TIME

The following section is a version of a manuscript to be submitted for publication

As the lead author of this article I am responsible for this manuscript. My primary contributions to this paper included the experimental design, data collection and analyses, and writing.

Abstract

Belowground foraging shapes ecosystem structure and function worldwide; however it is unknown what the consequences are if such foraging is performed by invasive mammals. Using a large-scale exclosure experiment we investigated the impact of belowground foraging by wild boar (*Sus scrofa*) on soil physical proprieties, plant community structure and composition, and on decomposition rates. We measured soil temperature, moisture, and compaction, recorded plant composition, and collected aboveground biomass in boar-rooted, experimentally rooted, and no-rooting (exclosure) plots. Also, we set up a leaf litter decomposition experiment and retrieved the litter bags after 4 and 8 months in the field. We found that rooting by wild boar reduced soil compaction by 5%, reduced aboveground plant biomass 3.8-fold decreasing grass and herb cover, and reduced decomposition rates by 5%. Taken together these results suggest that belowground foraging by wild boar may slow organic matter turnover in the long term.

Key words: wild boar, belowground herbivory, soil properties, decomposition rates.

Introduction

Belowground foraging by mammals is an important driver of ecosystem structure and function across ecosystems worldwide (Andersen 1987, Whitford and Kay 1999, Gutiérrez and Jones 2006). However, it is unknown how belowground foraging by non-native mammals influences invaded ecosystems. While foraging or constructing burrows, mammals move and mix soil from different horizons, altering nutrient distribution and subsequent plant community composition and chemistry (Tardiff and Stanford 1998, Sirotnak and Huntly 2000, Reichman and Seabloom 2002, Canals et al. 2003, Gutiérrez and Jones 2006). For example, grizzly bear diggings increase N content 1.3-fold for re-vegetating glacier lilies influencing the long- and short-term plant community structure in subalpine meadows of the USA (Tardiff and Stanford 1998). Similarly, foraging pits of echidnas increase soil respiration by 30% in a semi-arid woodland in Australia (Eldridge and Mensinga 2007). Moreover, rooting disturbance by native wild pigs decreases the number of seedlings by 56% shaping the structure of the Malysian rainforest (Ickes et al. 2001). While it is clear that native belowground herbivores shape ecosystem structure and processes, we know less about the ecosystem consequences of non-native species introducing a novel disturbance such as belowground foraging.

Invasive species are a major driver of ecosystem-change. For example, rat predation on seabirds disrupted a sea-to-land nutrient subsidy system, reducing soil fauna abundance and basal respiration, while increasing litter decomposition rates on New Zealand islands (Fukami et al. 2006). Similarly, earthworm introduction increased basal microbial respiration 5-fold and enhanced organic C availability via processing and mixing litter in the mineral soil in northern hardwood forests of the USA (Li et al. 2002). Even though there is some evidence on how belowground foraging by non-native mammals can alter plant community composition and nutrient availability (Bratton 1975, Singer et al. 1984, Kotanen 1995, Tierney and Cushman 2006), the consequences for ecosystem processes such as decomposition remain unknown. Previous work on native mammals has shown that belowground foraging disrupts the soil structure, altering properties such as soil moisture, temperature, and compaction (Huntly and Reichman 1994), stimulating microbial activity (Eldridge and Mensinga 2007), increasing the surface area available to decomposers (Sherrod and Seastedt 2001), and accelerating the rates of organic matter decomposition. However, the extent to which belowground foraging by non-native mammals will have such impacts is unknown.

Animal invasions may alter litter decomposition directly by reducing plant litter quantity or indirectly by altering the controls of litter decomposition (Ehrenfeld 2010). Selective browsing and the production of secondary compounds can lead to shifts in plant composition towards dominance of well-defended plants with poor litter quality, hence poor decomposability (Pastor et al. 1993). However, belowground foraging might alter decomposition rates by changing other factors than litter chemistry. The rate of litter decomposition is known to increase with temperature and with the number of trophic levels, species identity, and the presence of keystone species in the decomposer community (Kirschbaum 1995, Hättenschwiler et al. 2005). Soil microclimate and the composition of the decomposer community could be altered by the destructive habit of belowground foraging, yet there is no evidence of these changes by non-native mammals.

Using a large-scale exclosure experiment across three different ecosystem types, we investigated how belowground foraging by invasive wild boar (*Sus scrofa*) alters (1) soil physical properties, (2) plant community structure and composition, and (3) decomposition rates. Because rooting by wild boar targets roots, disrupts soil structure, and mixes soil horizons, we hypothesized that rooting will (1) increase soil temperature and decrease soil moisture and compaction, and (2) decrease plant cover, altering plant species composition, and that (3) rooting disturbance will increase decomposition rates.

Methods

This study was conducted on Isla Victoria (3710 ha), Nahuel Huapi National Park in northwestern Patagonia, Argentina (40°57' S; 71°33' W). Mean annual precipitation is 1700 mm and mean annual temperature is 8°C. Soils are young Andisols derived from postglacial volcanic ashes classified as Hapludands and Udivitrands (Ayesa et al. 2002). The island is mainly covered by three dominant plant communities, pure stands of the conifer *Austrocedrus chilensis*, pure stands of the evergreen southern beech *Nothofagus dombeyi*, and shrublands co-dominated by *Lomatia hirsuta* and *Maytenus chilensis.* The understory plant composition varies by dominant overstory species, but it is generally dominated by the shrubs *Schinus patagonicus* and *Berberis darwini*, herbs, and graminoids. Wild boar (*Sus scrofa*) colonized Isla Victoria in 1999 and their activity has increased since their introduction, which indicates an increase in population size (MNBG personal observation); however, there is no information on how boar disturbance varies across the island.

In 2008, we established exclosures to test experimentally how foraging disturbance by wild boar alters the structure (plant community composition and biomass) and function (decomposition) of these ecosystems. Based on observations that wild boar activities vary with plant community type across the island, we established our exclosures in the three dominant plant communities: *Austrocedrus* forests, *Nothofagus* forests, and shrublands. Within each of these plant communities, we established 10 circular exclosures (11 m^2) in areas with no visible rooting activity. Exclosures were established at least 100 meters apart, fenced with 1-m high woven wire and a strand of barbed wire at ground level along the perimeter to prevent boar from prying up the fencing (Tierney and Cushman 2006). Each exclosure was randomly divided into four quarters: one quarter ($2.75m^2$) was experimentally disturbed with a shovel by overturning the first 10 cm of the soil profile, while the other three quarters were maintained intact (Figure III.3). We conducted the experimental disturbance one time, in 2008, to tease apart the effect of soil disturbance from other impacts that wild boar might have on the plant community or decomposition rates. Each exclosure was surrounded (0.5 m apart) by 4 open plots (11 m^2) in order to monitor plant community and ecosystem responses to boar activity (Figure III.3). Unless otherwise noted, data were collected during the austral summer of 2011.

To assess the effect of rooting treatments (boar rooting, experimental rooting, and exclosure/ non-rooting) on plant communities, we harvested aboveground plant biomass at the end of the growing season (2011) in 0.5 × 0.5 m quadrats randomly placed within the three treatments. Harvested plant material was oven-dried for approximately 48 hours at 60˚C and weighed. We also conducted a field survey of rooting disturbance and plant composition by identifying plant species and visually estimating the relative abundance (% cover) in exclosure and surrounding open plots. Plant species were identified according to Ezcurra and Brion (2005).

Soil temperature (0-10 cm), moisture (0-12 cm), and compaction (0-15 cm) were measured in each of the three treatments in 6 of the exclosures in each of the plant communities. Soil temperature was taken with a digital soil thermometer, and soil moisture was measured with a TRIME-FM soil moisture device (Mesa Systems Co, USA). Soil compaction was assessed using an impact penetrometer (Synergy Resource Solutions Inc, USA), recording the cumulative number of strikes required for each 5 cm depth increment (5, 10 and 15 cm) (Herrick et al. 2005).

To investigate the effect of rooting treatments on decomposition rates, we set up a leaf litter decomposition experiment in 2010. The upper side of each 10 × 10 cm decomposition bag was constructed of 0.8 mm polyester mesh and the lower side (facing the ground) was constructed of 0.2 mm mosquito mesh. Bags were stitched together on three sides with polyester thread and closed with stainless steel staples. Leaf litter used to fill decomposition bags was collected in nylon mesh collectors suspended beneath the crowns of *Nothofagus dombeyi* trees over a period of four months (November 2009-February 2010). Dropped leaves were collected bimonthly, air-dried, combined, homogenized and sorted to remove any non-litter material. We used *N. dombeyi* as a standard local substrate because we were interested in assessing the impact of rooting disturbance on decomposition, rather than differences due to litter quality or plant community type. Furthermore, *N. dombeyi* is the only dominant plant species that releases leaves continuously throughout the year. Decomposition bags contained 3 grams of leaf litter and were placed in the three treatments. We set out the litter bags in February 2010 and retrieved and weighed them after 4 and 8 months in the field (July and November 2010). In total, we placed 162 decomposition bags (3 treatments x 27 exclosures x 2 collection dates).

Data analyses

To test the effects of rooting treatments (boar rooting, experimental rooting, and exclosure/no rooting) and plant community type (*Austrocedrus* forest, *Nothofagus* forests and shrubland) on plant biomass, soil moisture, soil temperature, soil compaction, and decomposition rates we used two-way ANOVA and Tukey-Kramer post hoc tests to compare means. Plant composition changes were analyzed with PERMANOVA using the Bray–Curtis dissimilarity matrix on log-transformed abundance data (Primer-E). To explore the relationship between rooting and changes in plant cover of functional groups, we used linear regressions. In this analysis we included the 4 open surveyed plots (4 open plots, 10 replicates, 3 plant communities = 120), in which rooting varied from 0 to < 50%. When it proved necessary, data were log-transformed to meet normality assumptions; however, figures show untransformed mean values. Data from 27 of the exclosures were used, as three shrubland exclosures had no rooting activity after the exclosure establishment in 2008. All statistical analyses were conducted using JMP Pro 10 statistical software with alpha set *a priori* as $\alpha < 0.05$ (SAS Institute, Pacific Grove, CA, USA, 2001).

Results

We analyzed the effects of the rooting treatments and plant community type on our response variables independently because we did not find any significant interaction terms (Underwood 1996).

Effects on plant community composition and structure

Rooting by wild boar reduced aboveground plant biomass 3.8-fold relative to the exclosure, and 2.3-fold relative to the experimentally rooted areas (two-way ANOVA, $p<0.001$, $F_{8,80} = 8.630$, Figure III.3 and III.4A), and there was a significant community type effect: plant biomass was ~1.5-fold greater in *Austrocedrus* forests and shrublands compared to *Nothofagus* forest. Furthermore, plant composition differed significantly across rooting treatments (PERMANOVA, pseudo $F = 1.941$, $p=0.0140$) and community type (PERMANOVA, pseudo $F = 40.407$, $p= 0.0001$): rooting disturbance reduced grass and herb cover ($p<0.001$, $R^2= 0.187$; $p=0.049$, $R^2= 0.034$ respectively, Figure III.4B and C) with a concomitant increase in bare soil ($p < 0.001$, $R^2 = 0.163$).

Effects on soil properties

As expected, rooting by wild boar decreased soil compaction (0-5 cm) by 5% in relation to experimental rooting and exclosure plots (two-way aANOVA, $p< 0.001$, $F_{8,53}=5.549$) but had no effect on compaction of deeper soil layers (Table III.2). There was a community type effect, indicating greater soil compaction in shrublands than in *Austrocedrus* and *Nothofagus* forests. Interestingly, soil temperature and moisture were not altered by wild boar rooting (Table III.2), but varied significantly only across community type, showing greater temperature and moisture in shrublands (21.5±0.9 °C, 13.8±1.2%) in relation to *Austrocedrus* (16.2±03°C, 6.5±0.3%) and *Nothofagus* (15.4±0.3 °C, 8.2±0.6%) forests.

Effects on decomposition rates

Surprisingly, litter mass loss was 5% slower in boar-rooting plots in relation to experimental rooting and exclosure plots (two-way ANOVA, p = 0.012, $F_{8,80} = 2.674$, Figure III.5), and did not vary across community type (p=0.144).

Discussion

We used a large-scale exclosure experiment to test how wild boar rooting activity was alerting plant community structure and composition, and decomposition rates across three plant community types. We found that belowground foraging by wild boar reduced soil compaction by 5%, altered plant community structure by decreasing plant biomass 60%, altered plant composition by decreasing grass and herb cover, and reduced litter decomposition rates by 5%. These results provide new evidence on the effects belowground foraging by invasive mammals may have and suggest that wild boar may decrease soil organic matter turnover in the long term.

Rooting by wild boar reduced soil compaction but had no effect on soil microclimate (moisture and temperature). Because belowground foraging disrupts soil structure, we hypothesized that rooting would increase soil temperature and decrease soil moisture. However, previous work on wild boar also found no differences in soil moisture in grasslands and oak woodlands in the USA (Moody and Jones 2000, Cushman et al. 2004, Tierney and Cushman 2006), while the only record from the native range found significantly lower soil moisture in rooted parches compared to non-rooted patches, and no effects on soil temperature (Risch et al. 2010). In light of the fact that rooting disturbance by wild boar decreased soil compaction of the upper soil layer (0-5 cm), it could possibly be that in fact rooting does not alter the overall soil microclimate conditions. Alternatively, moisture and temperature differences between rooting and no-rooting patches may vary appreciably during certain seasons.

As in other studies, we found that wild boar reduced plant biomass by 60% and cover of grass and herbs suggesting that rooting has comparable impact across ecosystems. Previous studies show that rooting reduces plant cover and diversity, altering plant community composition (Bratton 1974, 1975, Singer et al. 1984, Kotanen 1995, Hone 2002, Tierney and Cushman 2006, Siemann et al. 2009). For example, Bratton (1975) reported that understory cover was reduced by 90% in gray beech forest of the USA. Moreover, Cushman et al. (2004) found that rooting disturbance increased exotic plant species richness by 29%, altering the composition of coastal grasslands in California. Overall, grasses and herbs were also the functional groups most commonly affected by rooting (Bratton 1974, 1975, Singer et al. 1984, Kotanen 1995, Hone 2002, Tierney and Cushman 2006).

The presence of wild boar slowed decomposition rates by 5%. While this may not seem to be a great effect, it could alter the C cycle over time. Previous studies reported that belowground foraging often results in increased decomposition rates, as organic material gets fragmented and buried, and soil disturbance stimulates microbial activity (Sherrod and Seastedt 2001). However, we found the opposite effect. Decomposition rates are determined by climate, litter quality, and the soil community. However, we did not detect differences in soil moisture, temperature, or nutrients (unpublished data), and we used the same litter across treatments. Therefore, rooting disturbance might be affecting the decomposer community. Enzymes of micro-organisms catalyze most of the chemical transformations at rates primarily determined by temperature and moisture conditions (Lavelle et al. 1997), which we found to be unaltered. Furthermore, nutrient cycling measurements (soil respiration and nitrogen mineralization) were similar in rooting and no-rooting patches (unpublished data), indicating that foraging disturbance might be affecting macro-organisms.

Prior studies show that wild boar prey on soil fauna and that trampling can reduce litter-dwelling animals by 10-fold (Howe et al. 1981, Baron 1982, Diong 1982, Pavlov and Hone 1982, Singer et al. 1984, Vtorov 1993, Taylor and Hellgren 1997, Sierra 2001, Skewes et al. 2007, Desbiez et al. 2009). Soil macrofauna (collembolans, isopods, annelids, insects, and earthworms) function as litter transformers and determine the rate of organic matter decomposition (Bradford et al. 2002, Bardgett 2005, Hättenschwiler et al. 2005, Bardgett and Wardle 2010). Specifically, soil macro-fauna fragment plant material increasing the surface area available for microbial colonization, partially digest dead plant matter increasing the surface-to-volume ratio, and bring internal and external microbes in contact (Bardgett and Wardle 2010). Although, it is accepted that the significant level of functional redundancy in the decomposer biota suggests little effect on decomposer processes (Wardle 2006), a reduction of soil fauna activity could explain the reduced rates of litter decomposition in our experiment. Future work should therefore evaluate the mechanism by which wild boar rooting might impact soil macro-organisms and the processes regulated by them.

Overall, our results show that belowground foraging by wild boar can disrupt ecosystem structure and process by decreasing plant primary productivity and decomposition rates. Although, the reduction of decomposition rates is not large, rooting might decrease soil organic matter turnover in the long term.

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Appendix III: Tables and Figures

Table III. 2. temperature and moisture. Results of two-way ANOVA for the effect of boar rooting, experimental rooting, and exclosure on soil properties (Error df= 45)

	Source	**df**	**F-ratio**	**p-value**
Soil compaction (0-5cm)	Treatment	2	11.650	**<0.001**
	Community	2	9.107	**<0.001**
	Interaction	4	0.720	0.582
Soil compaction (5-10cm)	Treatment	2	4.403	**0.018**
	Community	2	10.632	**<0.001**
	Interaction	4	0.412	0.799
Soil compaction (10-15cm)	Treatment	2	0.411	0.665
	Community	2	3.714	**0.032**
	Interaction	4	0.486	0.746
Soil temperature (0-10cm)	Treatment	2	0.090	0.913
	Community	2	28.334	**<0.001**
	Interaction	4	0.029	0.9983
Volumetric soil moisture (0-10cm)	Treatment	2	0.724	0.491
	Community	2	18.813	**<0.001**
	Interaction	4	0.633	0.641

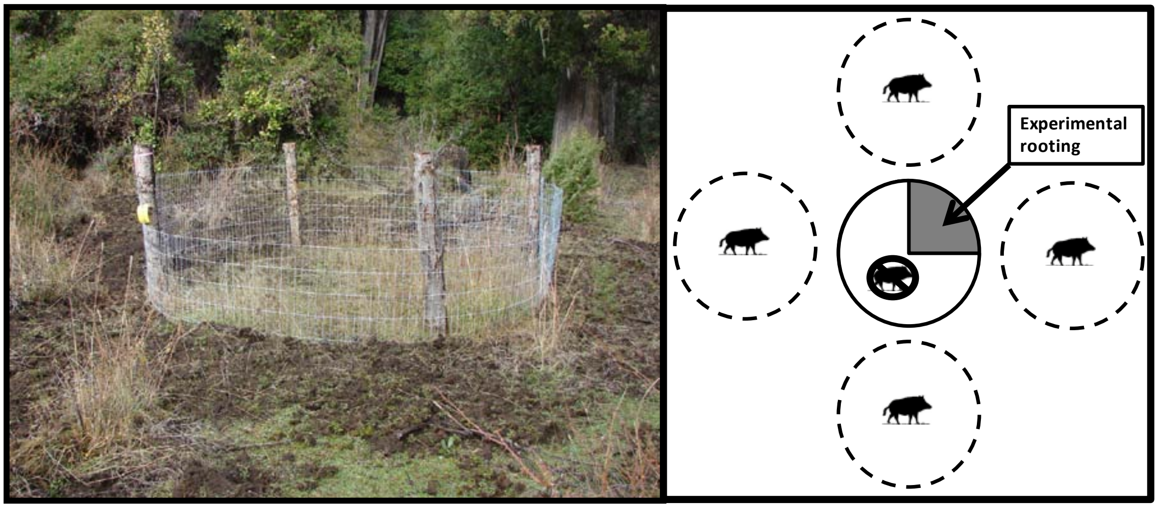

Figure III.3. Wild boar rooting in shrublands reduces plant abundance, soil compaction, and decomposition rate. The boar exclosure in this photograph is 11 m^2 and had been established since 2008.

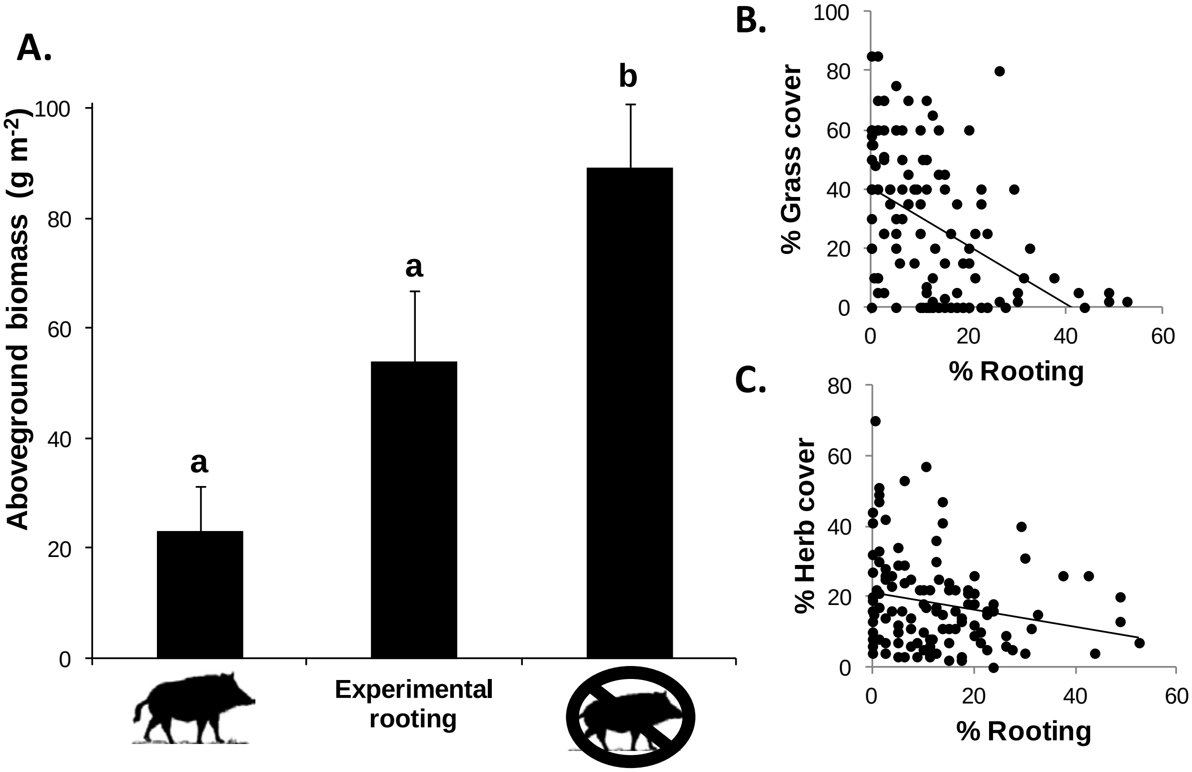

Figure III.4. Wild boar rooting decreases aboveground plant biomass 2.3 × relative to experimental rooting and 3.8 × relative to areas where they are excluded (A, mean ± SE, letters indicate significant differences among treatments). Both grass (B) and forb (C) functional groups decreased as rooting area increased (linear regressions, r2= 0.19 and 0.03 respectively).

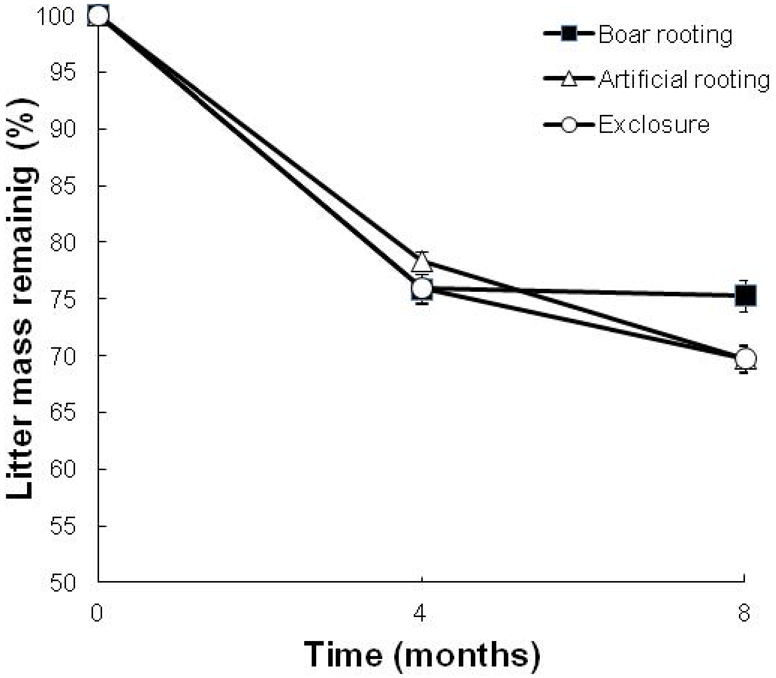

Figure III.5. Litter decomposition rates (% mass loss) were 5% lower in non-rooted areas than in rooted areas after 8 month (mean ± SE).

CHAPTER IV. PLANT COMMUNITIES, NOT BELOWGROUND HERBIVORY, SHAPES NUTRIENT PROPERTIES IN SOILS

The following section is a version of a manuscript to be submitted for publication.

As the lead author of this article I am responsible for this manuscript. My primary contributions to this paper included the experimental design, data collection and analyses, and writing.

Abstract

Plant community composition and belowground herbivory can both drive soil nutrient properties. However, it is unknown how they interact in natural systems. Using a large-scale wild boar (*Sus scrofa*) exclosure experiment on three ecosystem types, we aim (1) to assess the effects of ecosystem type and rooting disturbance by invasive wild boar on soil properties, and (2) to determine the spatial and temporal dynamics of rooting activity by wild boar across different ecosystems in NW Patagonia. We collected soil samples from exclosure (no rooting) plots, experimentally disturbed plots, and boar-rooted plots of different age, and we analyzed soil physical, chemical, and biological properties. By seasonal surveys we determined the spatio-temporal dynamics of rooting disturbance across ecosystems. We found that ecosystem type drives soil properties and functions more than rooting disturbance by boar regardless of time since disturbance. Furthermore, rooting by wild boar varied spatially and temporally, occurring at a greater rate in *Nothofagus* forests during winter and fall. These results suggest that plant nutrient inputs more strongly influence soil properties than herbivore nutrient outputs, which demonstrates the importance of comparing the influence of multiple biotic drivers on natural ecosystems. The spatio-temporal dynamics of rooting disturbance in the region provide insights on disturbance predictability, allowing us to identify which ecosystems are most prone to damage.

Keywords: biotic drivers, C and N content, N mineralization, soil respiration, wild boar, Patagonia

Introduction

Plant community composition and belowground herbivory can both drive soil nutrient properties, but the relative influence of the latter has not been explicitly tested. Plant community composition and belowground herbivory might have opposite effects on ecosystem properties, as plant communities modulate nutrient inputs to soils, whereas belowground herbivory affects nutrient outputs. Several studies have evaluated the influence of plant diversity and/or herbivory on ecosystem function (Pastor et al. 1993, Tilman et al. 1997, Wardle et al. 2004), yet how they interact in natural systems is still unknown. Moreover, it is possible that the outcome is exacerbated when the herbivores are non-native to the ecosystem.

The effect of plant species composition on ecosystem properties has traditionally been evaluated by manipulating plant diversity and functional traits. These experiments suggest that soil processes appear to be primarily influenced by the functional characteristics of dominant species rather than by the number of species present (Hooper et al 2005). For example, using a combination of 4 functional groups, Hooper and Vitousek (1997) showed that the soil nitrogen pool decreases as plant functional group richness increases owing to dominant effects of early season annuals in all mixtures of which they were a component. However, less is known about how multi-species natural communities influence soil properties (Bardgett and Wardle 2010) or the interaction of community composition with other biotic drivers such as herbivory.

Selective browsing can indirectly affect soil properties by affecting the quantity and quality of resources that plants produce. Specifically, there is evidence that herbivory in fertile ecosystems increases nutrient availability and mineralization rates while decreasing C sequestration; whereas the contrary is true for infertile ecosystems (Wardle et al 2004). However, belowground herbivory can influence ecosystem function by changing factors other than litter chemistry. Prior work has shown that belowground foraging can be an important force in pedogenesis, in structuring landscapes, and in maintaining ecosystem function (Whitford and Kay 1999). For example, belowground herbivory by pocket gophers (*Thomomys bottae*) can significantly lower soil organic matter, total C, total N, total P, and labile P, but increase plant-available P and NO_3, thus increasing ecosystem heterogeneity and nutrient redistribution (Sherrod and Seastedlt 2001). Still, many studies exploring the influence of belowground foraging on soil properties have found contrasting results (Singer et al. 1984, Moody and Jones 2000, Cushman et al. 2004, Tierney and Cushman 2006, Siemann et al. 2009). Part of the context-dependency may arise because belowground feeding disturbance effects may vary with ecosystem type (e.g., grasslands vs. forests) and with time since disturbance, as changes might fade as time proceeds (Sherrod and Seastedlt 2001). However, no studies include such comparisons.

Using a large-scale wild boar (*Sus scrofa*) exclosure experiment across three ecosystems, we aim (1) to assess the effects of ecosystem type and rooting disturbance by invasive wild boar on soil properties, and (2) to determine the spatio-temporal dynamics of rooting activity by wild boar in different ecosystems in NW Patagonia. We predict that, because belowground foraging mixes the upper layers of the soil profile, (1) rooting disturbance will have greater effects than ecosystem type on soil properties by increasing nutrient stocks and nutrient cycling rates compared to intact and old rooted patches, and (2) rooting will vary across season and ecosystem type.

Methods

Site description

This study was conducted on Isla Victoria (3710 ha), Nahuel Huapi National Park in northwestern Patagonia, Argentina (40°57’ S; 71°33’ W). Mean annual precipitation is 1700 mm and mean annual temperature is 8°C. Soils are young Andisols derived from postglacial volcanic ashes classified as Hapludands and Udivitrands (Ayesa et al. 2002). The island is mainly covered by three dominant ecosytems, pure stands of the conifer *Austrocedrus chilensis*, pure stands of the evergreen southern beech *Nothofagus dombeyi*, and shrublands co-dominated by *Lomatia hirsuta* and *Maytenus chilensis*. The understory plant composition varies by dominant overstory species, but it is generally dominated by the shrubs *Schinus patagonicus* and *Berberis darwini*, herbs, and graminoids. Wild boar (*Sus scrofa*) colonized Isla Victoria in 1999, and their activity has increased since their introduction, which indicates an increase in population size (MNBG *personal observation*); however, there is no information on how boar disturbance varies across the island and no estimate of boar population size

We established an exclosure experiment to assess spatial and temporal variation of rooting as well as rooting impact on soil properties of these ecosystems. Because we hypothesized that impact of wild boar may vary by ecosystem type, we replicated our exclosure experiment in the three dominant ecosystems: *Austrocedrus* forests, *Nothofagus* forests, and shrublands. Within each of these dominant ecosystems, we established 10 circular exclosures (11 m^2) in areas with no visible rooting activity, but that had a high likelihood of being damaged (determined by a rooting survey indicating that rooting disturbance is more frequent in areas with plant cover ranging from 20 – 50%, Barrios-Garcia *unpublished data*). Exclosures were established at least 100 meters apart, fenced with 1-m high woven wire and a strand of barbed wire at ground level along the perimeter to prevent wild boar from prying up the fencing (Tierney and Cushman 2006). Each exclosure was randomly divided into four quarters: one quarter (2.75m^2) was experimentally disturbed with a shovel by overturning the first 10 cm of the soil profile, while the other three quarters were maintained intact. We conducted the experimental disturbance once, in 2008, to tease apart the effect of soil disturbance from other impacts that wild boar might have on soil properties. Each of the exclosures is surrounded (0.5 m apart) by 4 open plots (11 m^2) where we recorded rooting temporal variation (% area disturbed) every season from spring 2008 to summer 2011.

Impact of rooting on soil properties

To determine the impact of rooting disturbance on soil properties we collected soil samples from the exclosure (no rooting), experimental disturbance, and boar-rooting patches of different age (determined by the seasonal surveys) in 6 exclosures per ecosystem type. We thought that the impact of rooting disturbance on soil properties might vary with time since disturbance, so we collected samples from fresh (2010) and old rooted patches (2008). Samples were collected in February 2011, consisting of 5 subsamples to 10 cm in depth. These were stored in sealed plastic bags and transported immediately to the laboratory.

1. Physical properties

Soil temperature (0-10 cm) was measured in the field with a digital soil thermometer. Field-fresh samples, sieved to pass through a 2 mm mesh, were employed to assess soil gravimetric water content (GWC) by oven-drying a 5 g subsample of soil for approximately 48 h at 105 °C. Air-dried soils sieved through a 2 mm mesh were used to assess pH in water (1:2.5).

2. Chemical properties

Air-dried soils sieved through a 2 mm mesh were used to assess P extractable in 0.5 M $NaHCO_3$ (1:20, soil:solution ratio) by the molybdate ascorbic acid method. Organic C and total N were analyzed in air-dried samples sieved to pass through a 0.5 mm mesh using a NC Soil Analyzer Flash EA 1112 at 900 °C combustion (Thermo Electron Corporation, USA).

3. Biological properties

Field-fresh samples, sieved to pass through a 2 mm mesh, were employed to assess potential microbial respiration and N mineralization. Potential microbial respiration was evaluated by determining CO_2 emission in 1.5-L glass jars, each containing a 75 g soil sample, incubated in the dark at 25 °C, and field capacity moisture for 40 days (Lerch et al. 1992). At 7, 16, and 40 days CO_2 was determined using vial traps of 0.2M NaOH. Respiration was estimated as the cumulative CO_2 evolution during the incubation period. Potential N mineralization was estimated after a 40-day incubation of 100-g samples in 0.25-L plastic jars. Inorganic N (Ni = NO_3^--N + NH_4^+ -N) was extracted at the beginning (t_0) and after 40 days (t_{40}) with 2M KCl (8 g soil and 40 mL extracting solution). NO_3^- -N was determined by copperized Cd reduction and NH_4^+ -N by the Berthelot reaction

(Keeney and Nelson 1982). Mineralization rates were calculated as the difference between Ni t_{40} - Ni t_0.

Data analyses

We analyzed the effects of disturbance treatment (exclosure/no rooting, experimental rooting, fresh and old rooting) and ecosystem type (*Austrocedrus* forest, *Nothofagus* forests and shrubland) on gravimetric water content, pH, total C, total N, extractable P, and nitrogen mineralization rate with two-way ANOVA and Tukey-Kramer post hoc tests to compare means. We log-transformed soil temperature, gravimetric water content, total C, extractable P, nitrogen mineralization, and soil respiration to meet normality assumptions. Soil respiration was analyzed with repeated measures ANOVA for treatment and ecosystem effects. To test the main and interactive effects of season and ecosystem type on percent rooted disturbance, we used a two-way ANOVA and Tukey-Kramer test. Rooted disturbance (%) from the exclosure experiment was log-transformed to meet normality assumptions. We also calculated the % annual rooted area by ecosystem type by adding the area rooted across seasons per ecosystem per year, and calculating an average using the data of 2009 and 2010 (the only years with data for all 4 seasons). All statistical analyses were conducted using JMP Pro 10 statistical software with alpha set *a priori* as $P < 0.05$ (SAS Institute, Pacific Grove, CA, USA, 2001).

Results

Impact of rooting on soil properties

Only ecosystem type, not wild boar rooting disturbance or their interaction, altered soil properties (Table IV.3). In particular, we found that temperature was ~5 °C higher in shrublands compared to *Austrocedrus* and *Nothofagus* forests, pH was highest in *Austrocedrus* forest (6.43), intermediate in *Nothofagus* forest (6.28), and lowest in shrublands (6.05); total C content was 30% greater in *Austrocedrus* and *Nothofagus* forest than in shrublands; extractable P was higher in *Nothofagus* forest (11.3 μg P/g), intermediate in *Austrocedrus* forest (7.50 μg P/g) and lower in shrublands (4.51 μg P/g); N mineralization was 2-fold higher in *Nothofagus* forest than in *Austrocedrus* forest and shrublands; while soil respiration was 2.3-fold higher in *Nothofagus* forest than in shrublands and 1.2-fold higher in *Nothofagus* forest than in *Austrocedrus* forest (Table IV.4, Figure IV.6).

Rooting dynamics

The exclosure experiment showed that rooting activity by wild boar varies significantly across seasons and ecosystems (Figure IV.7, two-way anova, $p<0.001$, $F_{32,1319}=23.42$). There were significant ecosystem, season, and interaction terms ($p_{ecosystem}<0.001$, $p_{season}<0.001$, and $p_{interaction}<0.001$). Rooting was greatest in *Nothofagus* forest, where an average of 72.5% of the surveyed area was annually rooted, followed by *Austrocedrus* forest and least in shrublands, where 35% and 34% of the surveyed area was annually disturbed, respectively (Figure IV.7). Rooting was greater in winter and fall followed by spring and summer (Figure IV.7).

Discussion

Our results show that ecosystem type drives soil properties and functions more than rooting disturbance by boar regardless of time since disturbance. Furthermore, rooting by wild boar varied spatially and temporally, occurring at a greater rate in *Nothofagus* forests during winter and fall. The result that soil properties and processes were more strongly influenced by ecosystem type rather than belowground foraging contradicts our prediction, as we expected that the disruption of the soil structure would alter soil functions. However, it sheds light on the importance of comparing the influence of multiple biotic drivers on ecosystem properties.

Our data indicate that rooting disturbance had no significant effect on soil properties and processes, while ecosystem effects prevailed. It was expected that rooting disturbance would increase nutrient availability and cycling, as rooting incorporates organic material from the litter layer into the mineral soil (Singer et al. 1984). However, we did not detect a significant effect of rooting on any of the soil measurements. Previous studies also show idiosyncratic results: rooting had increasing (Singer et al. 1984, Siemann et al. 2009), decreasing (Singer et al. 1984), or nil (Groot Bruinderink and Hazebroek 1996, Moody and Jones 2000, Cushman et al. 2004, Mohr et al. 2005, Tierney and Cushman 2006) effects on soil nutrient availability and cycling. We thought that this inconsistency might be due to variation across ecosystems, with some ecosystems responsive to rooting while others are not. However, we consistently found no effect of rooting disturbance on soil properties even when we accounted for ecosystem variability and time since disturbance.

The prevailing effect of ecosystem type on soil properties and functions with the absence of belowground responses due to herbivory has been previously observed. This is because nutrient availability and cycling are directly influenced by litter quality, which is indirectly influenced by aboveground herbivores. Previous studies have shown significant effects of plant canopy on soil processes such as N mineralization and soil respiration (Kieft 1994, Satti et al. 2003), as well as striking aboveground effects by herbivorous mammals that disappear belowground or have contrasting outcomes (Wardle et al. 2001, Canals et al. 2003, Stark et al. 2003). Moreover, plant species have been shown to have a greater effect than gopher disturbance on nitrogen cycling (Eviner and Chapin III 2005), suggesting that plant inputs have stronger influence on soil properties than do herbivores outputs.

The absence of response of soil properties to rooting disturbance could be explained by soil resilience and/or soil recovery. Soils in northwestern Patagonia are derived from volcanic ash with high capacity to stabilize soil organic matter, retain P and water, and buffer pH, which makes them highly resistant to nutrient loss (Diehl et al. 2003, Alauzis et al. 2004). Alternatively, given that rooting activity peaks in winter and that we collected the soil samples in summer, it could be that soil functions are recovered in that short period of time. However, this is unlikely given that when differences were detected, disturbance had long-lasting effects that disappeared 2 years after the rooting event (Risch et al. 2010). Furthermore, the impacts of rooting disturbance on soil properties might take more than one rooting event over long periods of time, and thus the effects of rooting might be measurable after several years of continuous disturbance. Future sampling will help to elucidate the matter.

Finally, our data indicate that rooting disturbance varies across seasons and ecosystem type. Rooting disturbance peaked during winter and fall and decreased during summer and spring. This pattern is consistent with previous studies showing the presence of underground plant material in stomach contents when aboveground resources are scarce (Genov 1981, Baron 1982, Herrero et al. 2004), but it is opposite to findings in New Zealand (Thomson and Challies 1988) and in the USA (Wood and Roark 1980, Taylor and Hellgren 1997), as roots were more commonly present in the stomachs during summer and spring in those studies. Furthermore, we found that rooting disturbance impact is greatest in *Nothofagus* forest compared to *Austrocedrus* and shrublands, as twice as much area is annually disturbed by wild boar. This finding is the first record of the spatial and temporal dynamics of rooting disturbance in the region and provides insights on disturbance predictability (Welander 2001) and allows us to identify which ecosystems are especially prone to damage (Baron 1982, Hone 1995, Mitchell et al. 2007).

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Appendix IV: Tables and Figures

Table IV. 3. Results from two-way anovas on soil physical, chemical, and biological properties. Soil respiration was analyzed with repeated measures anova. Bold numbers indicate significant differences ($P < 0.05$).

Variable	Source	d.f.	F	*P*
Physical				
Temperature (°C)	Treatment	3	0.077	0.972
	Ecosystem	2	31.210	**<0.001**
	Treatment* Ecosystem	6	0.070	0.999
Gravimetric water content (%)	Treatment	3	0.083	0.968
	Ecosystem	2	2.378	0.102
	Treatment* Ecosystem	6	0.116	0.994
Chemical				
pH	Treatment	3	0.651	0.585
	Ecosystem	2	13.850	**<0.001**
	Treatment* Ecosystem	6	0.295	0.937
Total C (%)	Treatment	3	0.540	0.657
	Ecosystem	2	17.566	**<0.001**
	Treatment* Ecosystem	6	0.645	0.694
Total N (%)	Treatment	3	0.285	0.836
	Ecosystem	2	2.382	0.102
	Treatment* Ecosystem	6	0.420	0.862
Extractable P (µg P/g)	Treatment	3	0.905	0.962
	Ecosystem	2	17.716	**<0.001**
	Treatment* Ecosystem	6	0.881	0.514
Biological				
N min (µg N/g)	Treatment	3	0.796	0.501
	Ecosystem	2	50.651	**<0.001**
	Treatment* Ecosystem	6	0.554	0.764
Soil respiration (CO_2 mg kg^{-1} soil)	Treatment	3	0.438	0.736
	Ecosystem	2	25.969	**<0.001**
	Treatment* Ecosystem	6	0.777	0.584

Table IV. 4. Mean (± standard error) for temperature, gravimetric water content, pH, C content, N content, extractable P, and N mineralization by ecosystem type. Different letters indicate significant differences at $p<0.05$.

	Austrocedrus forest	*Nothofagus* forest	Shrubland
Temperature (°C)	16.22 (0.32) b	15.39 (0.29) b	21.51 (0.90)a
Gravimetric water content (%)	22.65 (1.63) a	27.43 (1.76) a	25.65 (1.48) a
pH	6.43 (0.05) a	6.28 (0.06) b	6.03 (0.03) c
C (%)	11.00 (0.55) a	10.36 (0.45) a	7.48 (0.29) b
N (%)	0.61(0.03) a	0.58(0.03) a	0.52 (0.03) a
Extractable P (μg P/g)	7.50 (0.63) b	11.3 (1.23) a	4.51 (0.60) c
N Mineralization (μg N/g)	44.05 (2.95) b	87.27 (4.55) a	38.46 (2.43) b

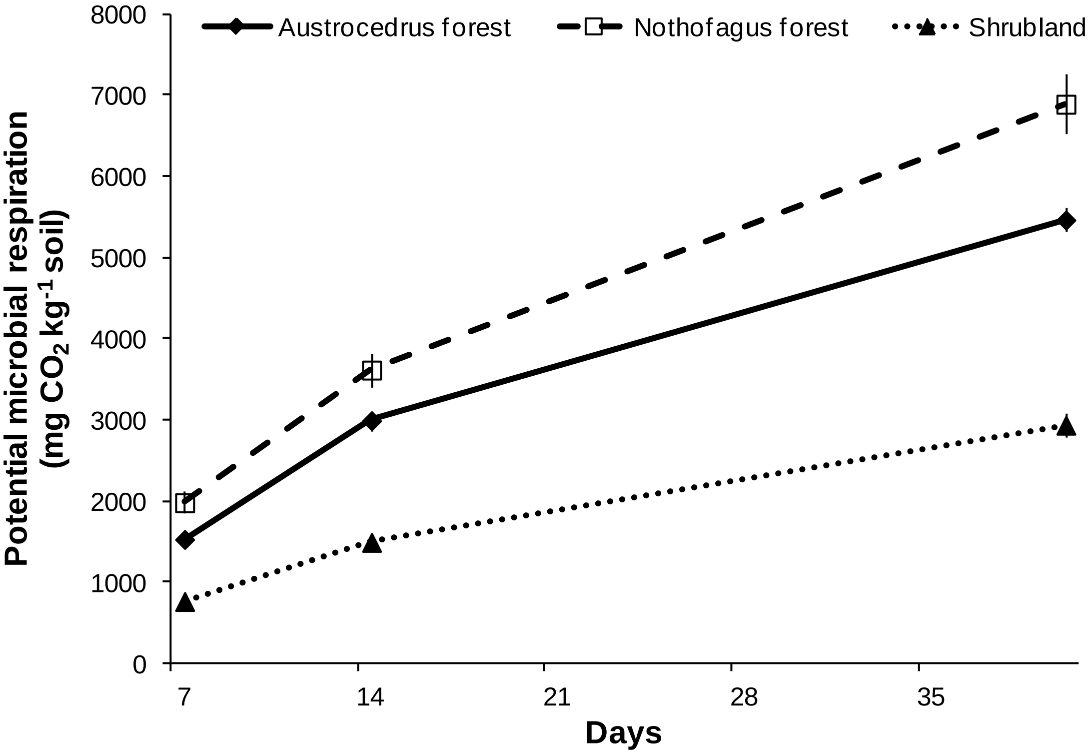

Figure IV.6.Potential microbial respiration varies significantly with ecosystem type.

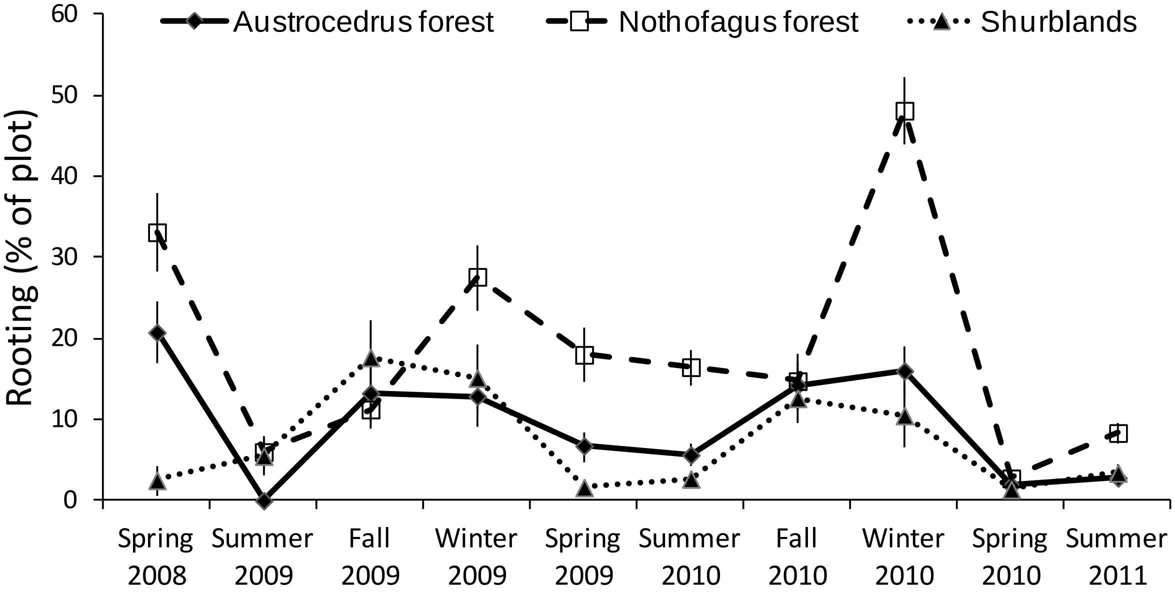

Figure IV.7.Rooting activity varies across seasons and ecosystem type. Error bars indicate standard error.

CHAPTER V. LINKING THE PATTERN TO THE MECHANISM: HOW AN INTRODUCED MAMMAL FACILITATES PLANT INVASIONS

The following section is a slightly modified version of a paper submitted in the journal Austral Ecology:

Barrios-Garcia, M.N and D. Simberloff (*in review*) Linking the pattern to the mechanism: how an introduced mammal facilitates plant invasions

As the lead author of this article I was responsible for this paper. My primary contributions to this paper included the experimental design, data collection and analyses, and writing.

Abstract

Non-native mammals that are disturbance agents can promote non-native plant invasions, but to date there is scant evidence on the mechanisms behind this pattern. We used wild boar (*Sus scrofa*) as a model species to evaluate the role of non-native mammals in promoting plant invasion by identifying the degree to which soil disturbance and seed dispersal drive plant invasions. To test if soil disturbance promotes plant invasion, we conducted an exclosure experiment in which we recorded emergence, establishment, and biomass of seedlings of seven non-native plant species planted in no-rooting, boar-rooting, and artificial rooting patches in Patagonia, Argentina. To examine the role of boar in dispersing seeds we germinated viable seeds from 181 boar droppings and compared this collection to the soil seed bank by collecting a soil sample adjacent to each dropping. We found that both establishment and biomass of non-native seedlings in boar-rooting patches were double those in no-rooting patches. Values in artificial rooting patches were intermediate between those in boar-rooting and no-rooting treatments. By contrast, we found that the proportion of non-native seedlings in the soil samples was double that in the droppings, and over 80% of the germinated seeds were native species in both samples. Lastly, an effect size test shows that soil disturbance by wild boar rather than dispersal facilitates plant invasions. These results have implication for both ranges of wild boar, where rooting disturbance may facilitate community composition shifts.

Key-words: facilitation, seed dispersal, soil disturbance.

Introduction

Positive interactions among non-native species, such as facilitation, have received increasing attention in the last decade (Simberloff and Von Holle 1999, Simberloff 2006). Additionally, non-native species that are disturbance agents may affect community invasibility and further exacerbate invasion by other species (Stone 1985, Vitousek 1990). However, in many cases the mechanisms by which facilitation among non-native species occurs are unclear. Non-native mammals can facilitate plant invasion by two main mechanisms: (1) altering disturbance regimes and/or (2) dispersing their seeds.

Natural disturbance plays a key role in maintaining diversity and functioning of native ecosystems (Connell 1978), but it can also enhance the abundance and distribution of non-native plants (D'Antonio et al. 1999). For example, disturbance by feral water buffalo is a major contributor to invasion by non-native weeds in Australia (Cowie and Werner 1993). Furthermore, seed dispersal is crucial for maintaining community structure and regeneration (Fragoso and Huffman 2000, Galetti et al. 2001, Trakhtenbrot et al. 2005); yet this same process might also accelerate invasion by non-native plants (Bourgeois et al. 2005). For example, Bourgeois et al. (2005) showed that seed ingestion by introduced rats and rabbits enhanced percent seed germination and speed of germination of the invasive succulents *Carpobrotus edulis* and *C. aff. acinaciformis* on French islands.

Identifying the mechanisms by which non-native mammals promote plant invasions has been hindered by the fact that it is difficult to tease apart mechanisms such as soil disturbance and seed dispersal (Kotanen 1995, Schmidt et al. 2004, Tierney and

Cushman 2006) or because mechanisms have been tested in isolation from each other. For example, wild boar (*Sus scrofa*) is a major disperser and facilitator of plant invaders (Vitousek et al. 1997, Simberloff and Von Holle 1999, Cushman et al. 2004). However, Aplet et al. (1991) noted that the non-native community composition in rooted areas by wild boar may be both the cause of rooting and the consequence of rooting. In other words, presence of non-native species may result from localized soil disturbance, or wild boar can be drawn to those sites (Aplet et al. 1991). Here, we aim to disentangle the relative importance of soil disturbance and seed dispersal by wild boar in promoting plant invasion.

In order to feed on belowground plant parts, fungi, and invertebrates, wild boar overturn extensive areas of vegetation (Baubet et al. 2003). This disturbance directly affects above- and belowground ecosystem components and may trigger plant invasion (Hobbs and Huenneke 1992, Kotanen 1997, Tierney and Cushman 2006). Although rooting creates suitable sites for colonization for both native and introduced plant species, it is likely that non-native plants colonize these disturbed areas more rapidly than native species (Aplet et al. 1991, Cushman et al. 2004, Hierro et al. 2006, Tierney and Cushman 2006). Furthermore, previous research has shown that wild boar in both their native and introduced ranges disperse seeds of native and non-native plant species (Lynes and Campbell 2000, Heinken and Raudnitschka 2002, Schmidt et al. 2004), but no information is available about the relative importance of boar dispersal to dispersal rates due to other agents or in relation to soil disturbance.

This study was conducted on Isla Victoria, Patagonia, Argentina, which was colonized by wild boar in 1999. The recent arrival of boar on the island provides an ideal opportunity to assess the mechanism by which non-native mammals promote plant invasion. Particularly, we tested the effect of soil disturbance on non-native seedling establishment and growth and the role of boar as a seed disperser in comparison to dispersal by other agents. To our knowledge this is the first study testing for different mechanisms explaining how non-native mammals facilitate plant invasions.

Methods

Study system

Wild boar are native to Eurasia but are now present on all continents except Antarctica, as well as on many oceanic islands (Long 2003). In Argentina, wild boar were introduced for sport hunting in La Pampa in 1904 and in Neuquen in 1917. However, after subsequent spread, the current distribution includes all of central Argentina and temperate forests of Patagonia (Novillo and Ojeda 2008). Wild boar were first recorded on Isla Victoria (3710 ha), Nahuel Huapi National Park, Argentina, in 1999 and currently attain high population densities (pers. obs.).

We conducted this study in three of the most common forest communities in Patagonia, *Nothofagus dombeyi* forest, *Austrocedrus chilensis* forests, and shrublands, which are co-dominated by *Lomatia hirsuta* and *Maytenus boaria*. The forest understory varies among communities but is generally dominated by the bamboo *Chusquea culeou* and the shrubs *Schinus patagonicus* and *Berberis darwinii*. Rooting disturbance occurs in all plant communities in a similar fashion (Barrios-Garcia, unpublished data).

Soil disturbance and plant invasion

To test if wild boar promote plant invasion through soil disturbance, we conducted an exclosure experiment in areas with no signs of boar rooting. In 2008 we set up ten circular matched triplets of 11 m^2 plots in each of the three community types (*Nothofagus* forest, *Austrocedrus* forest, and shrubland; N = 30) in areas with no rooting activity, but with high likelihood of ultimately being damaged by wild boar. One plot was fenced with 1-m high woven wire (10 by 5 cm mesh), while another plot with similar characteristics was open to allow boar access. Additionally, we artificially disturbed a third adjacent plot with a shovel, mimicking boar disturbance as closely as possible (11 m^2 patch, ~7 cm depth), to disentangle the effect of soil disturbance from other impacts that boar might have on the soil. In 2009, we planted 20 seeds of each of seven invasive non-native plant species inside (no-rooting) and outside (boar-rooting) 27 exclosures as well as in artificially rooted patches. We used data from 27 of the 30 exclosures because no rooting disturbance has occurred in the vicinity of three exclosures since we established them in 2008. We used seeds of trees, shrubs, and herbs that are most successfully invading the region (*Pinus ponderosa, Pseudotsuga menziesii, Juniperus communis, Cytisus scoparius, Rubus sp., Rosa rubiginosa, Carduus sp.*) We planted the seeds in the most freshly rooted patch (<6 months) recorded for each exclosure by seasonal surveys. We also set up smaller protections (50 cm in diameter and 20 cm high, using the same woven wire as for the exclosures) over the planted seeds to prevent further rooting disturbance outside the exclosures as well as inside the exclosures. We conducted yearly surveys in 2010 and 2011 to estimate seedling emergence and establishment. At the end of the growing season in 2011, we collected the aboveground parts of the seedlings and oven-dried and weighed the samples after 48 hrs at 60 °C.

Seed dispersal and plant invasion

To study the role of wild boar in facilitating non-native plant seed dispersal, we collected ~35 fresh boar droppings per month during the fruiting season 2010 (December, 2009 - April, 2010, N = 181). Samples were collected in the immediate vicinity of one large disturbed area where several exotic plant species are abundant. As a control, adjacent to each dropping we collected a soil sample with the natural seed bank containing all the seeds that could have been dispersed by seed dispersers or other means. Samples were approximately 10 by 10 cm and included the top 10 cm of the soil layer. Samples were air-dried, weighed to standardize the number of seeds per gram of sample, and cold-stratified for one month (Schmidt et al. 2004, Eycott et al. 2007). The number of viable seeds in each dropping and soil sample was determined by greenhouse germination. We mixed the samples with a constant amount of multipurpose compost and watered the containers to maintain moisture. At the end of the growing season of 2011, after 12 months of this set-up, we identified seedlings to species level when possible (undetermined seedlings were excluded from the statistical analysis).

Statistical analyses

The total numbers of seedlings growing in the boar-rooting, no-rooting, and artificial-rooting patches were log-transformed to meet normality assumptions and analyzed with a repeated measures MANOVA to test for the effects of community, treatment, and the interaction between them. Once we found non-significant interaction terms, we used one-way ANOVA blocked on exclosure, and Tukey-Kramer post hoc tests. Blocked ANOVA allows block differences to be removed, and the comparison of treatments under more uniform conditions. Total biomass was log-transformed to meet normality assumptions and analyzed with two way-ANOVA and Tukey-Kramer post hoc tests to test for treatment and community effects. All ANOVA analyses were completed in JMP Pro 9 (SAS Institute Inc., Cary NC). To determine if wild boar are more likely to disperse non-native than native seeds in comparison to the proportions available in the soil samples, we used Fisher's exact test. Fisher's exact test tests for frequency data and is more accurate than chi–square when one is dealing with two-by-two contingency tables. Furthermore, we compared the variation in species abundance and composition among sampling units (soil and droppings) with an analysis of similarity using a Bray-Curtis similarity matrix (ANOSIM) (Primer v6, PRIMER-E, Plymouth). Finally, to determine the relative importance of soil disturbance and seed dispersal by wild boar on non-native plants we calculated the effect size as the log-response ratio (ln *R*),

$$\ln R = \ln\left(\frac{\overline{X}^{P}}{\overline{X}^{A}}\right)$$

where X^P is the mean of the response variable mediated by wild boar and X^A is the mean of the response in the absence of wild boar (Hedges et al. 1999, Osenberg et al. 1999). Specifically, we used the number of non-native seedlings in boar-rooting and no-rooting patches (soil disturbance), and the number of non-native seedlings/gram from droppings and soil samples (seed dispersal). A response ratio of 0 (or if the standard deviation overlaps 0) indicates that wild boar had no effect on non native-plants. A positive response ratio indicates that wild boar facilitate non-native plants, while negative effect size shows a proportional negative effect on non-native plants.

Results

Soil disturbance and plant invasion

The numbers of non-native seedlings were three and two times higher in boar-rooting patches than in no-rooting patches in 2010 and 2011, respectively (Figure V.8; one-way ANOVA, 2010: $F_{2,52} = 14.99$, $P < 0.001$; 2011: $F_{2,52} = 4.02$, $P = 0.023$). There was a significant year effect produced by the germination of more seeds in 2011, but non-significant community effects or interaction terms (repeated measures MANOVA, TableV.5). Additionally, establishment of non-native species in artificial rooting patches was intermediate with respect to no-rooting and boar-rooting patches (Figure V.8). All the introduced species except for *Rosa rubiginosa* and *Rubus sp.* showed higher establishment in boar-rooting and artificial rooting patches than in no-rooting patches (Supplementary material, Table V.A8). Furthermore, biomass per individual seedling was three times higher in boar-rooting patches than in no-rooting patches, and artificial rooting patches had intermediate values (Figure V.9). There was a significant treatment and community effect, but no significant interaction (two-way ANOVA, Table V.6). The Tukey-Kramer post hoc test revealed larger biomass of seedlings growing in shrublands than in *Nothofagus* or *Austrocedrus* forests.

Seed dispersal and plant invasion

Overall 883 seedlings, comprising 27 species, were identified from the 362 soil and dropping samples. The proportion of non-native seedlings was two times greater in the soil samples than in the droppings, and over 80% of the germinated seeds were from native species in both samples (Fisher's exact test, $P < 0.001$, Table V.7). Thus, to the extent that wild boar are dispersing seeds, they are favoring natives over non-natives. Furthermore, similarity analysis showed that species composition of soil and dropping samples did not differ (ANOSIM, $P = 0.082$) (Species list in Supplementary material, Table V.A9).

Mechanisms' relative importance

The effect size shows that soil disturbance by wild boar has a positive and stronger effect than seed dispersal in facilitating non-native plants (Figure V.10).

Discussion

Non-native mammals can promote plant invasions (Simberloff and Von Holle 1999, Cushman et al. 2004), but to date there has been little evidence on the underlying mechanisms. Our results show that, for wild boar, soil disturbance rather than seed dispersal promotes the establishment and growth of non-native plants. We found two times greater establishment and biomass of non-native seedlings in boar-rooting patches compared to no-rooting ones. Furthermore, the fact that seedlings in the artificial rooting patches performed relatively poorly than those in the boar-rooting patches suggests that wild boar are causing other changes in soil properties than just mixing the soil horizons.

Soil disturbance such as rooting activity by wild boar has long been identified as a major disturbance with drastic ecosystem effects (Crooks 2002, Walker 2012). Yet most studies compared rooted to intact areas, without previous information on the affected area (plant composition or age of rooting disturbance). Therefore, it was difficult or impossible to determine if plant invasion was the cause or the consequence of soil disturbance (Aplet et al. 1991). Our results clearly show that soil disturbance is the main mechanism by which wild boar promote plant invasion. This result resembles those of previous studies in the USA showing that soil disturbance by native gophers facilitates invasion by exotic plants such as *Bromus mollis* and *Carpobrotus edulis* (Hobbs and Mooney 1991, D'Antonio 1993). However, our results involve facilitation among non-native species. Additionally, we found that non-native seedlings grew larger in shrublands than in the other plant communities, suggesting that in Patagonia invasion risk might be greater for this transitional ecosystem.

Enhanced plant establishment and performance of non-native seedlings on boar-rooted patches could be a result of (1) increased soil nutrient availability and/or (2) reduced herbivory by soil biota. To date, there is no agreement on the effects of rooting on soil properties. Previous research shows idiosyncratic changes in nutrient content and cycling as well as in physical soil properties (Singer et al. 1984, Moody and Jones 2000, Cushman et al. 2004, Tierney and Cushman 2006, Siemann et al. 2009). Furthermore, there are no data on the impacts of rooting disturbance by wild boar on soil invertebrates (nematodes, mites, collembola, earthworms, etc.) and the effect these impacts might in turn have on plant establishment. Future research should therefore explore possible mechanisms by which rooting enhances plant establishment and growth.

Our results from the seed dispersal experiment showed that wild boar favor natives over non-natives. Previous research in Australia has shown that wild boar successfully disperse seeds of non-natives (Grice 1996, Lynes and Campbell 2000). However, the lack of comparison to dispersal rates due to other agents may have led to an overestimate of the impact of wild boar as seed dispersers. The comparison of viable seeds from droppings and the seed bank of adjacent soil samples in our experiment clarifies the role of seed dispersal by boar. Surprisingly, most of the seedlings identified from the droppings were grasses and herbs, which suggests that seeds were probably accidentally ingested while boar were rooting for other resources (e.g., roots, fungi, earthworms). It is possible that the role of seed dispersal by wild boar becomes more important in places with higher abundance or diversity of fleshy-fruited plants. For example, there is some evidence that wild boar eat and disperse fruits of the invasive strawberry guava (*Psidium cattleianum*) in Hawaii (Diong 1982).

Our research highlights the importance of testing multiple contributing factors simultaneously and making appropriate comparisons. To date, parts of the mechanisms tested in this study have been investigated in isolation, preventing identification of the mechanism underlying the association of non-native mammals and plant invasion. Also, by studying non-native species in a recently colonized area, we were able to tease apart the mechanisms involved in facilitating plant invasion, which would have been difficult in areas where the animals had been long established.

Finally, this study provides insight for the development of management tools. Most studies focus on direct impacts of non-native mammals, but indirect effects might be as strong and important as direct effects. Here, we found that rooting disturbance by wild boar indirectly enhances non-native plant establishment and growth. This result has significant implications for both the native and introduced ranges of wild boar, where rooting disturbance can cause plant communities to shift towards non-native dominance. Therefore, most attention should be given to protected areas in the vicinity of sites dominated by non-native plants, as these species might rapidly colonize and exploit newly disturbed patches.

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Appendix V: Tables and Figures

Table V. 5.The number of non-native seedlings varied significantly across treatments (boar-rooting, no-rooting, and artificial rooting) and years (2010 and 2011, repeated measures MANOVA).

Source	df	F	*P*- value
Treatment	2	8.74	**0.0004**
Community	2	1.97	0.1471
Time	1	12.04	**0.0009**
Treatment*community	4	1.18	0.3253
Treatment*time	2	2.36	0.1021
Time*community	2	1.30	0.2776
Treatment*community*time	4	1.11	0.3564

Table V. 6.The biomass of non-native seedlings varied significantly across treatments (boar-rooting, no-rooting and artificial rooting) and plant communities (*Austrocedrus* and *Nothofagus* forest, and shrublands, two-way ANOVA).

Source	df	F	*P*- value
Treatment	2	4.54	**0.0139**
Community	2	27.39	**< 0.0001**
Treatment*community	4	4.27	0.0694

Table V. 7.The proportion of non-native seedlings was two times greater in the soil samples than in wild boar droppings, and most germinated seeds were native species in both samples (Fisher's exact test).

Sample	Origin		
	Native	Non-native	*P* – value
Dropping	300	22	<0.001
Soil	466	95	<0.001

Supplementary material

Table V.A 8. Average number of individuals (SE) and average biomass (SE) of the non-native species sown in the three treatments in the different plant communities.

		Average number of individuals						
Community	Treatment	*P. men.*	*P. pon.*	*J. com.*	*C. sco.*	*Rub. sp.*	*R. rub.*	*Car. sp.*
Austrocedrus forest	Artificial rooting	0.80 (0.47)	0.10 (0.10)	1.00 (0.52)	1.80 (0.85)	0.10 (0.10)	1.10 (0.41)	1.70 (0.70)
	Boar Rooting	0.70 (0.33)	2.00 (1.06)	0.60 (0.50)	1.10 (0.35)		1.10 (0.69)	1.30 (0.54)
	No Rooting	0.20 (0.13)	0.10 (0.10)		1.90 (0.67)		1.10 (0.46)	0.80 (0.51)
Nothofagus forest	Artificial rooting	1.00 (0.33)	1.80 (0.68)	1.00 (0.37)	1.50 (0.67)		0.80 (0.33)	0.30 (0.21)
	Boar Rooting	1.30 (0.67)	3.90 (1.36)	0.90 (0.41)	2.40 (0.64)		0.10 (0.10)	0.10 (0.10)
	No Rooting	1.10 (0.43)	0.80 (0.70)	1.30 (0.78)	1.80 (0.44)			
Shrubland	Artificial rooting	1.43 (0.87)	0.57 (0.20)	0.43 (0.30)	1.57 (0.92)		1.71 (0.92)	2.86 (0.77)
	Boar rooting	1.14 (0.46)	4.00 (1.73)	1.00 (0.58)	1.14 (0.63)		1.29 (0.57)	3.86 (0.59)
	No rooting	0.29 (0.18)	0.71 (0.42)	0.57 (0.43)	0.43 (0.30)		1.14 (0.63)	0.86 (0.55)

Table V.A8 Continue

Community	Species	Average biomass per individual (grams)						
		P. men.	*P. pon.*	*J. com.*	*C. sco.*	*Rub. sp.*	*R. rub.*	*Car. sp.*
Austrocedrus forest	Artificial rooting	0.06 (0.02)	0.03 (0.00)	0.01 (0.00)	0.01 (0.00)	0.01 (0.00)	0.02 (0.00)	0.08 (0.05)
	Boar rooting	0.03 (0.01)	0.08 (0.01)	0.01 (0.00)	0.01 (0.00)		0.01 (0.00)	0.28 (0.07)
	No rooting	0.04 (0.00)	0.09 (0.00)		0.01 (0.00)		0.02 (0.00)	0.02 (0.01)
Nothofagus forest	Artificial rooting	0.05 (0.01)	0.07 (0.01)	0.01 (0.00)	0.02 (0.00)		0.02 (0.00)	0.05 (0.01)
	Boar rooting	0.03 (0.01)	0.11 (0.01)	0.01 (0.00)	0.02 (0.00)		0.01 (0.00)	0.10 (0.00)
	No rooting	0.04 (0.01)	0.09 (0.02)	0.01 (0.00)	0.02 (0.00)			
Shrubland	Artificial rooting	0.05 (0.01)	0.21 (0.05)	0.01 (0.00)	0.08 (0.05)		0.03 (0.02)	0.91 (0.35)
	Boar rooting	0.05 (0.01)	0.23 (0.05)	0.02 (0.01)	0.02 (0.00)		0.02 (0.00)	1.31 (0.31)
	No rooting	0.08 (0.03)	0.14 (0.06)	0.01 (0.00)	0.08 (0.07)		0.02 (0.00)	0.48 (0.44)

Table V. A9.Proportion of species identified in soil and droppings; non-native species are marked with an asterisk (total seedlings in soil= 561 and in droppings= 322)

Species	**Soil**	**Dropping**
Acaena pinnatifida		0.003
Arenaria serpyllifolia *		0.006
Aristotelia chilensis	0.005	
Caiophora silvestris		0.006
Capsella bursapostoris *	0.038	
Carduus sp. *	0.002	
Cynanchum diemii	0.002	
Cytisus scoparius *	0.014	0.006
Galium sp.	0.005	
Graminoids	0.511	0.515
Hydrocotyle chamaemorus	0.019	0.009
Lotus pedunculatus *		
Montia perfoliata	0.010	
Mutisia spinosa		0.003
Nothofagus dombeyi	0.003	
Plantago lanceolata *	0.002	0.003
Pseudotsuga menziesii *		
Rosa rubiginosa *	0.003	
Rubus ulmifolius *	0.031	0.003
Rumex sp. *	0.016	0.009
Solanum sp.	0.017	0.003
Sonchus sp. *	0.058	0.031
Stellaria sp.	0.240	0.385
Taraxacum officinale *		0.003
Unicinia sp.		0.003
Viola sp.	0.002	

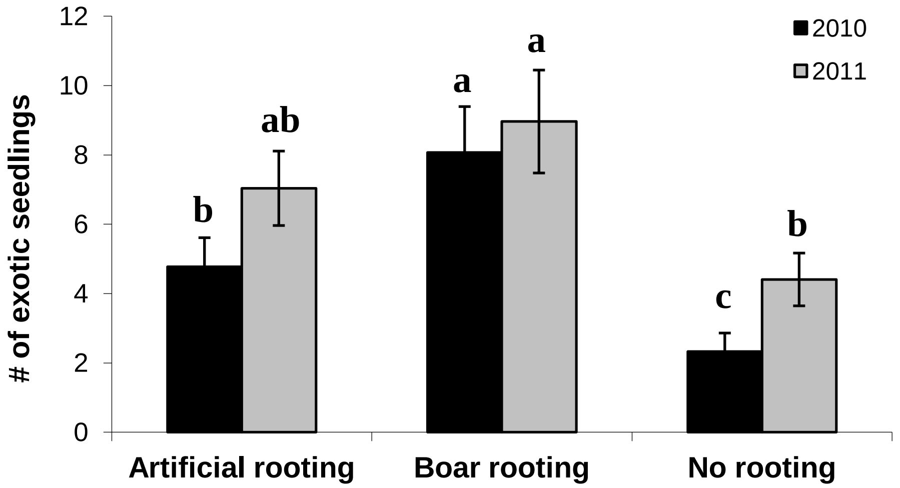

Figure V.8. The number of non-native seedlings that established in boar-rooting patches is three times higher than in no-rooting patches, and intermediate for artificial-rooting patches. Different letters indicate significant statistical differences among treatments at $P < 0.05$.

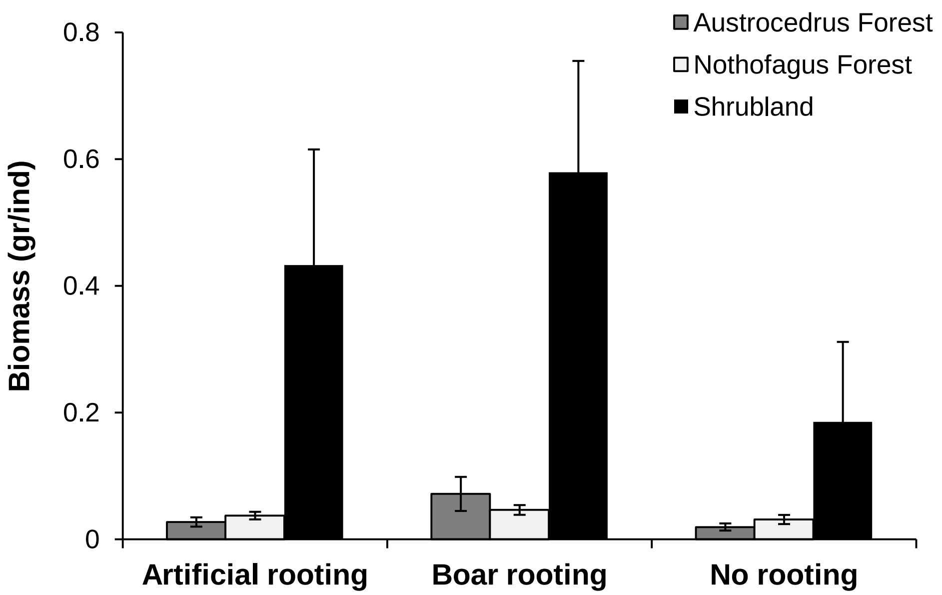

Figure V.9. Aboveground biomass per individual is greater in boar-rooting patches than in no- rooting patches; artificial-rooting patches are intermediate. Community effects show that biomass is greater in shrublands than in *Nothofagus* and *Austrocedrus* forests.

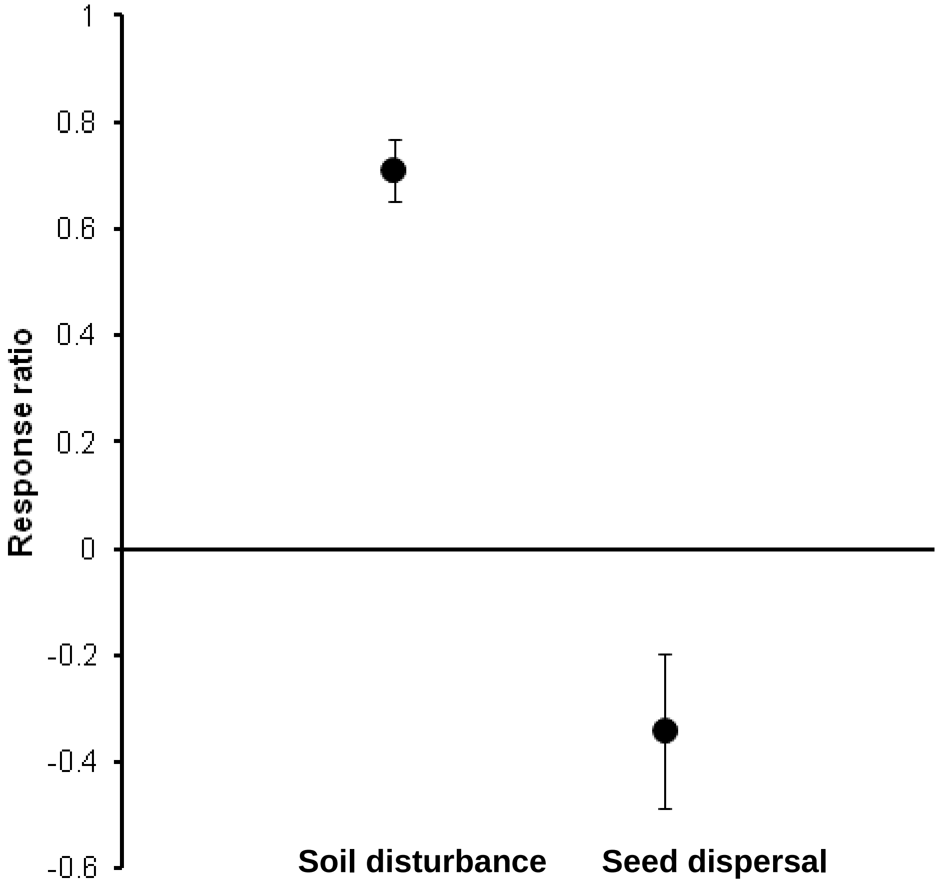

Figure V.10. The effect size shows a positive effect of soil disturbance by wild boar on non-native plants relative to seed dispersal. We calculated the effect size using the log response ratio; symbols represent the mean effect size and error bars standard deviation.

CHAPTER VI. CONCLUDING REMARKS AND FUTURE DIRECTIONS

Taken together, my dissertation shows how wild boar negatively affect both community and ecosystem properties in Patagonia by altering plant community composition and structure, reducing decomposition rates, and promoting invasive plant establishment and growth. These results are extremely useful for local National Park administrators as they now have an accurate assessment of the impact of wild boar in the area, which can be used to target control efforts to manage wild boar populations more effectively. My findings also provide additional support to the notion that invasive species impacts extend beyond those at the population level, and that above- and below-ground components are closely interlinked. However, my research has also generated new questions that will probably be the subject of future work in my lab.

1. As suggested in Chapter III, decomposition might be closely linked to soil macro-fauna presence/activity. Local hunters told me about stomachs full of earthworms during the fall (rainy season); hence future research should address the impact of rooting disturbance on soil macro-fauna richness and abundance.
2. Even though we did not detect any effect of rooting on soil properties, we found significant reduction in decomposition rates. As suggested in Chapter IV, soil functions might recover in that short period of time (6 months). Therefore, future work would include measuring soil process under field conditions right after disturbance or across seasons. Alternatively, another way to detect the effects of rooting on microbial activity would be through the assessment of enzyme activity.
3. In the field I observed dung beetles using wild boar feces, but I have not done any measurement of the consequences of such interaction. The role of dung beetles

might be important as they relocate nutrients, accelerate nutrient cycling rates, and enhance plant growth.

4. Wild boar invasion does not occur in isolation from interacting species, both native and introduced. To me it is fascinating to disentangle species' direct and indirect interactions as they occur simultaneously in an environment that is also subject to anthropogenic changes. Therefore, I would like to further explore the web of interactions to assess both evident and less obvious effects of invasions.
5. Finally, in the literature review in Chapter II, I found that we usually know a lot about the impact of wild boar and how to control them, but we know little about the consequences of controlling or removing wild boar in an already disturbed ecosystem.

Vita

Maria Noelia Barrios Garcia Moar was born in Buenos Aires, Argentina on March 31st, 1981. She attended the first 4 years of elementary school in Buenos Aires, then moved to San Carlos de Bariloche, Rio Negro, Argentina, where she graduated from high school. In 2005 she received the degree of Licenciada en Ciencias Biologicas from the Universidad Nacional del Comahue, where she studied the impact of introduced deer on different plant communities in Northwestern Patagonia. In August 2007, she started the Ph.D. program in Ecology and Evolutionary Biology at the University of Tennessee, Knoxville. The doctoral degree was awarded in December 2012