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Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review

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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

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Introduction

Wild boar (also known as feral pig or wild hog, *Sus scrofa*), native to Eurasia, are now present on all continents except Antarctica, and many oceanic islands (Long 2003; Fig. 1), 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

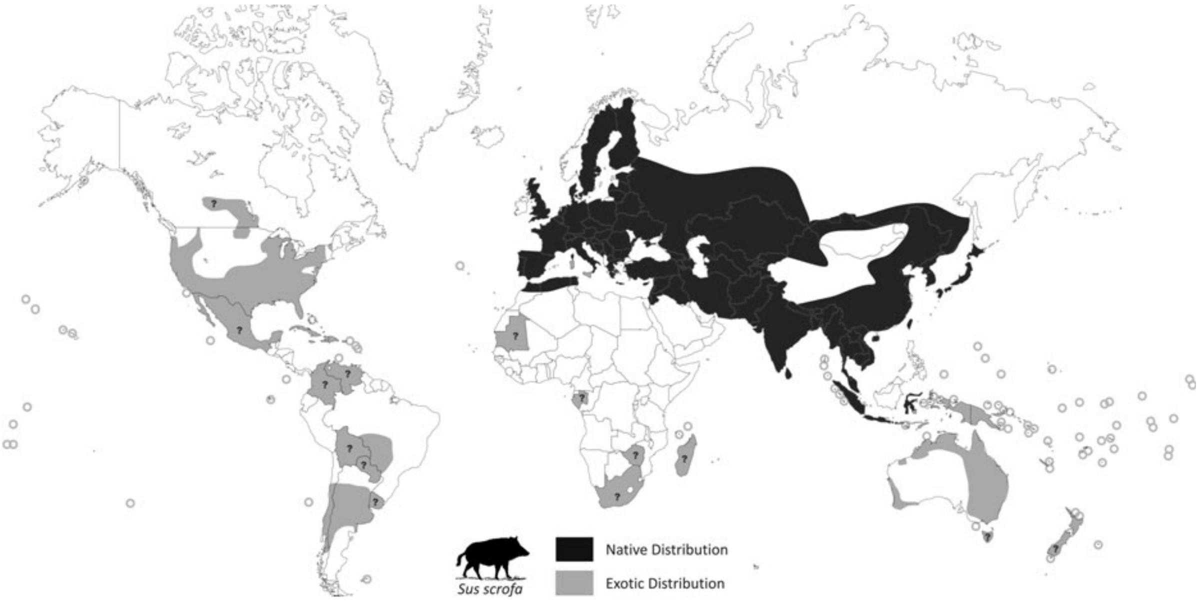

Fig. 1 Worldwide distribution of *S. Scrofa*. The species native range demarked in *black* and introduced range in *gray*. *Gray circles* indicate the islands where *S. scrofa* have been introduced. (?) denotes occurrence but unknown distribution

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 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,

Table 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)
Chemical properties				
pH	Introduced	Experimental	0	Moody and Jones (2000)
Nutrient content	Introduced	Descriptive/experimental	0/+/–	Singer et al. (1984), Moody and Jones (2000)
Biological properties				
N mineralization	Introduced	Experimental	+/0	Cushman et al. (2004), Siemann et al. (2009)
Soil respiration			?	
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 endozoochory	Native/introduced	Descriptive	Native & invasive sp.	Lynes and Campbell (2000), Heinken et al. (2002)
Dispersal ectozoochory	Native	Descriptive	+	Heinken and Raudnitschka (2002)
Animal communities				
Predation				
Invertebrates	Introduced	Descriptive	–	Challies (1975), Taylor and Hellgren (1997)
Vertebrates	Introduced	Descriptive	–	Coblentz and Baber (1987), Jolley et al. (2010)
Effects on pop dynamics			?	
Habitat and nest destruction	Introduced	Descriptive	–	van Riper and Scott (2001)
Competition	Native/introduced	Descriptive/experimental	–/0	Focardi et al. (2000), Desbiez et al. (2009)
Hybridization	Native	Descriptive	–	Blouch and Groves (1990), Long (2003)

Table 1 continued

Impact	Study area	Type of evidence	Effect	Representative references
Fungi community				
Mycophagy	Native/introduced	Descriptive	Occurs	Fournier-Chambrillon et al. (1995)
Dispersal	Native/introduced	Descriptive	?/+/−	Genard et al. (1988)
Aquatic communities				
Plant community				
Plant cover	Introduced	Descriptive/experimental	−	Arrington et al. (1999), Doupé et al. (2010)
Species diversity	Introduced	Descriptive/experimental	+/−/0	Arrington et al. (1999)
Animal community				
Predation				
Invertebrates	Introduced	Descriptive/experimental	+/−/0	Kaller and Kelso (2006), Doupé et al. (2010)
Vertebrates	Native/introduced	Descriptive	−	Genov (1981)
Dispersal				
Plants	Native/introduced	Descriptive/experimental	Invasive sp.	Setter et al. (2002)
Invertebrates	Native	Descriptive	+	Vanschoenwinkel et al. (2008)
Water quality and chemistry				
Nutrients	Introduced	Descriptive/experimental	+/0	Browning (2008), Doupé et al. (2010)
Effect on communities			?	
Other impacts				
Wallowing			?	
Rubbing trees	Introduced	Descriptive	−	Stegeman (1938), 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 (1993), Schley and Roper (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)

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. Mohr 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 2 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 (2000) found that wild boar in Australia disperse seeds 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 and 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 and 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 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) being 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 USA 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 USA (Wood and Barrett 1979; Graves 1984), squirrels and black bear in the US (Wood and Barrett 1979), cranes in the USA (Everitt and Alaniz 1980), and terrestrial vertebrates in California, USA (Sweitzer and Van Vuren 2002).

In their native range, wild boar also feed on species from all animal groups: invertebrates, amphibians, reptiles, mammals and birds (Genov 1981; Fournier-Chambrillon et al. 1995; Baubet et al. 2003; Schley and Roper 2003; Baubet et al. 2004; Herrero et al. 2004, 2005, 2006; Irizar et al. 2004; Mohr et al. 2005; 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, 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 ($\sim$60 %) than in the native range ($\sim$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 (*Annona glabra*) 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, 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, 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, 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*), a soil-borne plant pathogen. Li et al. (2010) show that *P. 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 (Roemer et al. 2002). 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 coryi*), 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 et al. (1999) found that wild boar rooting can increase plant-defined micro-habitat 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 1 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 populations (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—CA, USA (Barrett et al. 1988), Santa Catalina—CA, USA (Schuyler et al. 2002), Pinnacles National Monument—CA, USA (McCann and Garcelon 2008), Santa Rosa Island—CA, 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 % 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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