Do changes in soil properties after rooting by wild boars (*Sus scrofa*) affect understory vegetation in Swiss hardwood forests?

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Abstract: Recovering from small fragmented populations, wild boars (*Sus scrofa* L.) have considerably increased their numbers and their habitat range in many European countries during the past two decades. Although several studies have focused on the impact of wild boar rooting on selected vegetation properties, little is known about effects on entire forest ecosystems. The main goal of our study was to assess how rooting by boars alters soil and vegetation properties. We measured soil chemical and biological properties (C and N concentrations, N availability, and microbial biomass C) as well as several vegetation characteristics (total plant cover, plant species diversity, and number and height of saplings) on paired rooted and non-rooted plots in six hardwood forests in Switzerland. We found that rooting by wild boars led to significant increases in mineral soil C and N concentrations and microbial biomass C, which could lead to improved growth conditions for plants. However, total plant cover and sapling counts were reduced on rooted plots, possibly due to mechanical disturbance or due to reduced plant available N (measured as supply rate in contrast with the observed increase in total stocks of mineral soil N). In view of these results, simple characterizations of wild boar rooting as beneficial or detrimental to forest ecosystems should be handled with care.

Résumé : Après avoir récupérés à partir de petites populations fragmentées, les sangliers (*Sus scrofa* L.) ont considérablement augmenté leur nombre et l'étendue de leur habitat dans plusieurs pays européens au cours des deux dernières décennies. Bien que plusieurs études aient mis l'emphase sur l'impact de la fouille des racines par le sanglier sur certaines propriétés de la végétation, les effets sur les écosystèmes forestiers tout entiers sont peu connus. L'objectif principal de notre étude consistait à évaluer de quelle façon la fouille des racines par les sangliers modifie les propriétés du sol et de la végétation. Nous avons mesuré les propriétés chimiques et biologiques du sol (concentrations de C et de N, disponibilité de N et biomasse microbienne de C), ainsi que plusieurs caractéristiques de la végétation (couvert végétal total, diversité des espèces végétales et nombre et hauteur des gaules) dans des parcelles appariées avec et sans fouille des racines établies dans six forêts feuillues suisses. Nous avons observé que la fouille des racines par les sangliers entraînait une augmentation significative des concentrations de C et de N ainsi que de la biomasse microbienne de C dans le sol minéral, ce qui pouvait créer de meilleures conditions de croissance pour les plantes. Cependant, le couvert végétal total et le nombre de gaules étaient plus faibles dans les parcelles soumises à la fouille des racines, possiblement à cause de la perturbation mécanique ou de la moins grande disponibilité de N pour les plantes (mesurée par le taux d'apport, contrairement à l'augmentation observée dans les stocks totaux de N dans le sol minéral). À la lueur de ces résultats, on devrait éviter de simplement caractériser la fouille des racines par les sangliers de bénéfique ou de nuisible pour les écosystèmes forestiers.

[Traduit par la Rédaction]

Introduction

At the beginning of the last century, wild boars (*Sus scrofa* L.) were close to extinction throughout much of their natural range in Eurasia. Recovering from small, fragmented populations, wild boars have increased their numbers and their habitat range considerably in many European countries, including Switzerland, during the past two decades (Apollonio et al. 2010). Reasons for this widespread expansion include the boars' opportunistic feeding behavior, high reproductive potential, and adaptability to a wide variety of habitats (i.e., high ecological plasticity: Boitani et al. 1995; Taylor et al. 1998). Wild boars are omnivorous and obtain a considerable proportion of their diet by rooting (grubbing) in the soil searching for plant seeds, roots, bulbs, and vertebrate and invertebrate animals (e.g., Bratton et al. 1982; Baber and Coblenzt 1987; Hone 1988). Rooting involves breaking through the surface layer of vegetation followed by excavation of the detected food item, thereby disturbing up to 80% of the soil surface (Genov 1981; Howe et al. 1981; Risch et

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al. 2010). Excavation may be superficial, affecting the surface organic horizons only, but rooting typically affects the organic horizons and mineral soil combined to depths of 15 cm or more (Genov 1981; Kotanen 1995).

In temperate forests, boar rooting can have a large impact on C and nutrient cycling. The addition of energy-rich organic material mixed into the mineral soil alters C and nutrient concentrations (Nannipieri et al. 2003) and can stimulate microbial growth and activity (Mallik and Hu 1997) and therefore accelerate decomposition processes. Only a few researchers have investigated how rooting habits of wild boars affect forest soil C concentrations, nutrient cycling processes, or soil microbial properties (e.g., Groot Bruinderink and Hazebroek 1996; Mohr et al. 2005; Siemann et al. 2009) (see Table 1). These changes in soil properties could indirectly impact understory vegetation and (or) sapling growth, and wild boar rooting may also directly (and adversely) affect or damage the understory vegetation (e.g., through seed predation and mechanical damage). Several authors have studied how wild boar or feral hog populations alter understory plant cover (e.g., Peart and Patten 1992; Cuevas et al. 2010), plant community structure (e.g., Aplet et al. 1991; Siemann et al. 2009), and plant regeneration and growth potential (e.g., Lacki and Lancia 1986; Ickes et al. 2001; Sanguinetti and Kitzberger 2010) (see Table 1). In contrast, we only found three studies that investigated both above- and belowground parameters (Singer et al. 1984; Lacki and Lancia 1986; Groot Bruinderink and Hazebroek 1996) (see Table 1). These authors assessed the effects of wild boars on soil N and (or) organic matter (OM) concentrations as well as plant cover and regeneration and growth potentials, but none of these studies included nutrient dynamics and soil microbial properties. The goal of our study was to provide a more comprehensive understanding of how boar rooting might affect the entire plant–soil system by investigating rooting effects on soil chemical and biological properties (C and N concentrations, N availability, and microbial biomass C) as well as understory vegetation characteristics (total plant cover, plant species diversity, and number and height of saplings) in mixed hardwood forests, the forest types most frequently used as boar habitat in Switzerland.

Materials and methods

Study area and sampling design

The study was conducted in hardwood and mixed hardwood forests located north of Zurich (47°23′N, 8°31′E) in the state of Zurich, Switzerland. The mean annual temperature is 9.2 °C and the mean annual precipitation is 1137 mm (30 year averages from 1978 to 2008) with roughly 25% falling as snow during the months of November through February (MeteoSchweiz). We selected six 5 ha sites in European beech (*Fagus sylvatica* L.) dominated stands that also contained other hardwoods such as oaks (*Quercus* ssp.) and European hornbeam (*Carpinus betulus* L.), and conifers (Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.)). All six sites were classified as typical *Galio oderati – Fagetum* following Keller et al. (1998). The understory was dominated by tree saplings (mainly *F. sylvatica* and sycamore (*Acer pseudoplatanus* L.)), two perennial herbs (*Oxalis acetosella* L. and *Anemone nemorosa* L.), a perennial graminoid (*Carex pilosa* Scop.), and an annual herb (*Impatiens parviflora* DC.). All sites were located within 50 km of each other, with the closest distance between two sites exceeding 1 km. Elevations ranged from 550 to 670 m above sea level. All sites were located on sandy-loam textured soils with soil pH ranging between 2.7 and 3.6 (Table 2). Each forest site was inhabited by wild boars throughout the year and rooting was widespread. Risch et al. (2010) showed that 27.2%–53.8% of the forest soils of our sites were disturbed by boars between 2006 and 2008.

We established a paired-plot design consisting of a rooted (disturbed) and undisturbed plot in each of the six forests in early spring of 2006. Both plots were 10 m × 10 m in size and were fenced with 1.3 m high knotted mesh (Ursus 130/11/15; Hortima AG, Hausen, Switzerland: mesh size at 0–50 cm height = 10 cm × 15 cm, mesh size at 50–110 cm = 15 cm × 15 cm, and mesh size at 110–130 cm = 20 cm × 15 cm) tightened around 15 cm square wooden posts (1.6 m long) to prevent boars (and roe deer) from entering. Two 2.5 mm diameter wires were affixed at 1.4 and 1.5 m height to prevent other animals from jumping over the 1.3 m mesh. Measurements and soil sampling started just after plot establishments and were continued for up to 48 months (see details below).

Since rooting is generally visible for approximately 3 years in these forest types, our undisturbed plots had not been rooted for 3 years. To determine if boars specifically select foraging sites within a homogeneous stand or randomly grub in the soil, we established a third randomly chosen, non-rooted, and non-fenced 10 m × 10 m plot at each study site at the beginning of the study (May 2006). These random plots were all rooted by boars by the end of the study, and therefore, we assume that our randomly chosen non-rooted but fenced plots were sufficient to be compared with the respective rooted plots. However, we cannot rule out that some of the differences in ecosystem properties that we measured already existed prior to rooting. Unfortunately, such differences could not be accounted for because it is not possible to predict where the boars are going to root and therefore "pre-treatment" sampling was not possible (see also Risch et al. 2010).

Soil sampling and analyses

Soil sampling was conducted just after plot establishment in early June 2006 (time = 0 months) and again 2 years after plot establishment (time = 24 months). During each sampling campaign, we randomly collected three mineral soil cores (5 cm diameter) from each rooted and non-rooted plot at least 1 m from the fence to avoid edge effects. Samples were taken across a total depth of 45 cm after removing the organic horizons. Soil sampling was conducted at fixed depths with a soil corer (AMS, American Falls, Idaho), since no clear soil horizon delineation was possible after rooting. Subsamples were oven dried at 65 °C (for 48 h), passed through a 2 mm sieve, and finely ground. Total C and N concentrations were analyzed on a LECO induction furnace (LECO Corporation, St. Joseph, Michigan) at 950 °C. Values obtained from the three samples at each depth were averaged for each plot.

Microbial biomass was determined at 0 and 24 months using the substrate-induced method of Anderson and Domsch (1978). Fifty gram subsamples from all samples (pooled for

Table 1. Studies reporting wild boar (*Sus scrofa*) rooting effects on above- and belowground properties and processes.

Forest type	Wild boars	Soil N concentration	Soil N availability (flux)	Soil C concentration	Soil microbial biomass C	Total plant cover	Plant community structure	Plant growth	Forest regeneration potential	Source	Location
Mixed hardwood forest	Native	+	–	+	+	–	0	0	–	This study	Switzerland
Grassland and conifer forest	Native						+			Welander 1995	Sweden
Mixed hardwood and conifer forest	Native	0		0 (OM)				0	–/0	Groot Bruinderink and Hazebroek 1996	Netherlands
Hardwood (rain) forest	Native						+	–/0	–	Ickes et al. 2001	Malaysia
Hardwood forest	Native	–		–	–					Mohr and Topp 2001	Germany
Hardwood forest	Native	0		0	–/0					Mohr et al. 2005	Germany
Mixed woodland	Native								–	Gómez and Hódar 2008	Spain
Mixed hardwood forest	Native				+					Risch et al. 2010	Switzerland
Gray beech forest	Non-native					–				Bratton 1974	Tennessee, North Carolina
Gray beech forest	Non-native					–	–/0			Bratton 1975	Tennessee, North Carolina
Savannah, grassland, pine/shrub thicket	Non-native						0		0	Baron 1982	Mississippi
Rain forest	Non-native					0			–	Ralph and Maxwell 1984	Hawaii
Hardwood forest	Non-native	+/–				–				Singer et al. 1984	Tennessee, North Carolina
Hardwood forest	Non-native			+ (OM)				+		Lacki and Lancia 1986	Tennessee, North Carolina
Hardwood (rain) forest	Non-native						+/–/0			Aplet et al. 1991	Hawaii
Hardwood forest	Non-native					–			–	Peart and Patten 1992	California
Hardwood forest	Non-native	0 (nitrate)		0						Moody and Jones 2000	California
Oak woodland	Non-native								–	Sweitzer and Vuren 2002	California
Hardwood (rain) forest	Non-native								–	Mitchell et al. 2007	Australia
Mixed forest	Non-native					–	+	–	0	Siemann et al. 2009	Texas
Mast conifer forest	Non-native								–	Sanguinetti and Kitzberger 2010	Argentina
Hardwood woodland, shrubs, dunes	Non-native					+/–/0				Cuevas et al. 2010	Argentina

Note: +, positive effect; –, negative effect; 0, no effect found; blank cell, property not measured; OM, organic matter.

Table 2. Site and soil characteristics of the top 15 cm of the mineral soil for the six sites under study.

Site	Elevation (m)	pH	Available water (g·100 g soil^{-1})	Rock content (%)	Soil particle size distribution (%)			Soil texture class
					Sand	Silt	Clay	
1	550	3.12	20.41	41.90	73.2	18.0	8.8	Sandy loam
2	550	3.56	12.72	41.79	74.4	16.1	9.5	Sandy loam
3	560	2.81	12.60	33.46	75.8	17.1	7.1	Sandy loam
4	610	2.68	21.36	41.00	72.5	21.0	6.6	Sandy loam
5	650	2.69	21.09	17.58	67.2	26.0	6.8	Sandy loam
6	670	2.59	10.93	55.65	69.2	22.8	8.1	Sandy loam

Note: Soil pH was measured on a 2:1 water–soil paste.

each plot and sampling date) were immediately put on ice when collected, sieved through a 2 mm sieve, and stored in a cold room at 4 °C until further processing. Deionized water was added as needed to bring all samples to 60% water-filled pore space. The samples were then incubated at room temperature for 10 days prior to analysis to allow spurious microbial activity associated with the sampling disturbance to subside (to measure only basal respiration). Microbial biomass C was determined using 25 g of mineral soil (dry mass equivalent) and a glucose concentration of 5 g·kg soil^{-1}. CO_2 production was analyzed 1–2 h following the addition of glucose using a LI-COR 6200 gas analyzer (LI-COR Biosciences, Lincoln, Nebraska).

Nitrogen availability

To assess plant available total N (N supply rate as the sum of ammonium and nitrate) in the mineral soil, we incubated Plant Root Simulator probes (PRS; Western Ag Innovations Inc., Saskatoon, Saskatchewan) with ion-exchange resin membranes. At four randomly selected locations per plot, one pair of PRS probes, consisting of one anion and one cation probe, were inserted vertically into the soil. To ensure that membranes did not become saturated with ions absorbed from the soil, the probes were replaced with new probes (inserted into the same locations) every 6 weeks (time = 0 until time = 24 months, number of measurements = 15). Since it is important to avoid root competition (plant roots act as ion sinks, similarly to the PRS probes) during long-duration burials, we cut a 30 cm deep × 2 mm wide slit with a garden spade around the probes (square of 30 cm × 30 cm). Additionally, we continuously removed all plants growing within this square. In the laboratory, the PRS probes were cleaned thoroughly using toothbrushes and deionized water and were stored in labeled freezer bags at 4 °C in a cold room. At the end of the experiment, all samples were sent to Western Ag Innovations Inc. laboratory for analysis.

Vegetation sampling

All understory plant species were identified and the cover fraction of each species was quantified by visual estimation on four randomly selected 1 m × 1 m subplots within each rooted and non-rooted plot for three points in time: the initial survey after plot establishment at the beginning of the study (time = 0) and 12 months (time = 12) and 48 months (time = 48) later. Within each treatment, values of the four subplots were averaged. Plant species diversity was calculated as the Shannon index of diversity. Plant species richness was defined as the number of different plant species. Sapling abundance was determined by counting all saplings (less than 100 cm tall) and current-year seedlings. We also estimated total plant cover and measured the individual height of each sapling growing in each plot to the nearest centimetre. Height measurements of saplings at time = 12 and time = 48 were restricted to individuals taller than 10 cm to exclude seedlings grown after the initial survey. Saplings were not individually tagged.

Statistical analyses

A linear mixed-model procedure approach was used to test for treatment (rooted and non-rooted) and season (time) effects on mineral soil C and N concentrations, microbial biomass, N availability, total plant cover, plant species diversity, and number and height of saplings. These parameters were a function of the two fixed effects treatment (rooted and non-rooted) and time and the random effect site. We also adjusted this model for temporal autocorrelation using a first-order autoregressive (AR(1)) model, as the independence assumption of our data points in time was not met (Zuur et al. 2009). Because the vegetation data were strongly skewed and the sample sizes were small, the assumptions underlying traditional parametric statistics were not met. Thus, the continuous data were transformed to rank data using fractional ranking, which was then used in the same linear mixed-model approach as described above. All statistical analyses were performed with the R statistical package nlme version 2.4.1 (R Development Core Team 2006).

Results

Rooting effects on soil properties

Mineral soil C and N concentration and microbial biomass C (0–45 cm depth) were significantly higher on the rooted compared with the non-rooted plots (Table 3). Time effects could only be found for microbial biomass C, with significantly higher values measured 2 years after plot establishment (t = 24) compared with values measured immediately after plot establishment (t = 0) (Table 3). Nitrogen availability was significantly lower on the rooted plots (mean ± SE: 115.87 ± 23.74 μg·10 cm^{-2}·6 weeks^{-1}) compared with the non-rooted plots (160.06 ± 29.37 μg·10 cm^{-2}·6 weeks^{-1}) (number of measurements in each plot = 15) and varied significantly between the two sampling dates (Fig. 1).

Rooting effects on plant community properties

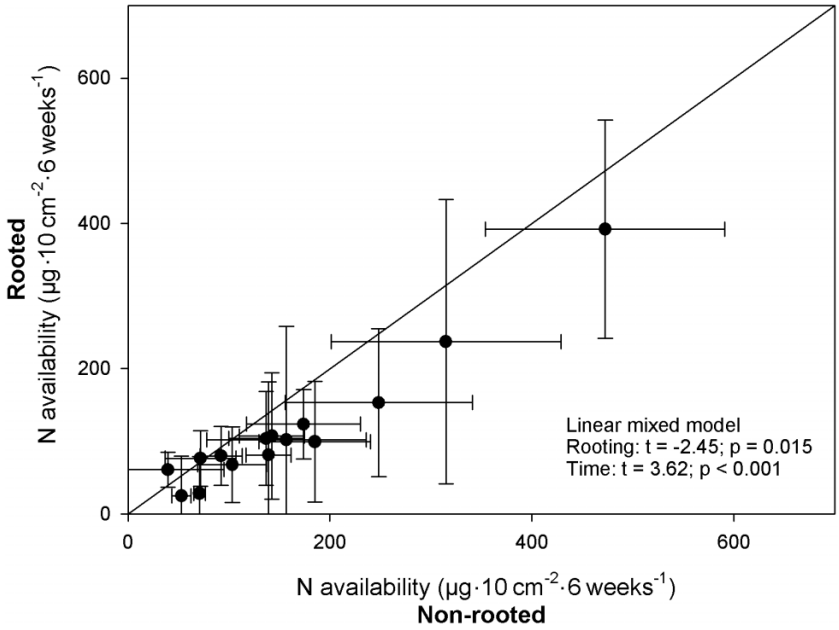
Total plant cover was significantly lower on the rooted plots compared with the non-rooted plots but did not signifi-

Table 3. Rooting and time effects on mineral soil C concentration, N concentration, and microbial biomass C.

	t = 0 months		t = 24 months		Rooting		Time	
	Rooted	Non-rooted	Rooted	Non-rooted	t	p	t	p
C concentration	3.05±0.39	2.36±0.24	3.81±0.8	2.7±0.35	–2.70	**0.02**	1.65	0.12
N concentration	0.15±0.02	0.12±0.01	0.18±0.03	0.14±0.01	–2.69	**0.02**	2.11	0.05
Microbial biomass C	822.67±94.18	541.01±80.81	1233.39±147.9	847.93±93.99	–3.40	**0.00**	3.65	**0.00**

Note: Values are means ± SE (n = 6) and t and p values of the linear mixed models.

Fig. 1. Plant available N measured on rooted and non-rooted plots between t = 0 and t = 24 months (n = 15). Data points represent the average ± SEs of all measurements made at the six rooted and non-rooted plots during one sampling occasion.



cantly vary between different sampling dates (Fig. 2). The same pattern was found for the number of saplings (Fig. 3). In contrast, we could not detect a rooting effect on sapling height, while sapling height varied significantly between different sampling dates (Fig. 4), indicating normal plant growth over time. Finally, plant species diversity (Fig. 5) showed no significant rooting effect and also no significant difference between the different sampling dates. In general, plant species richness was rather low on both rooted and non-rooted plots. Averaged over the three sampling events, we found only 5.03 different species on rooted plots and 5.00 different species on non-rooted plots.

Discussion

Our results showed that rooting by wild boars was associated with higher soil C and N concentrations and microbial biomass C. Together with the elevated CO_2 emissions detected on rooted plots in another subproject of the study (Risch et al. 2010), these findings suggest enhanced decomposition and faster turnover rates (mineralization) of C in rooted soils. Similar findings were reported by Lacki and Lancia (1983) who found higher OM concentrations in rooted compared with non-rooted plots in the Great Smoky Mountains National Park, USA (see also Table 1 for comparison of our data with those of other studies). The authors explained their findings by stimulated OM decomposition on boar-rooted sites. In contrast, in other studies (Groot Bruin-

Fig. 2. Total plant cover measured on rooted and non-rooted plots at time = 0, 12, and 48 months, respectively (n = 6 for all graphs). Data represent averages ± SEs of sites.

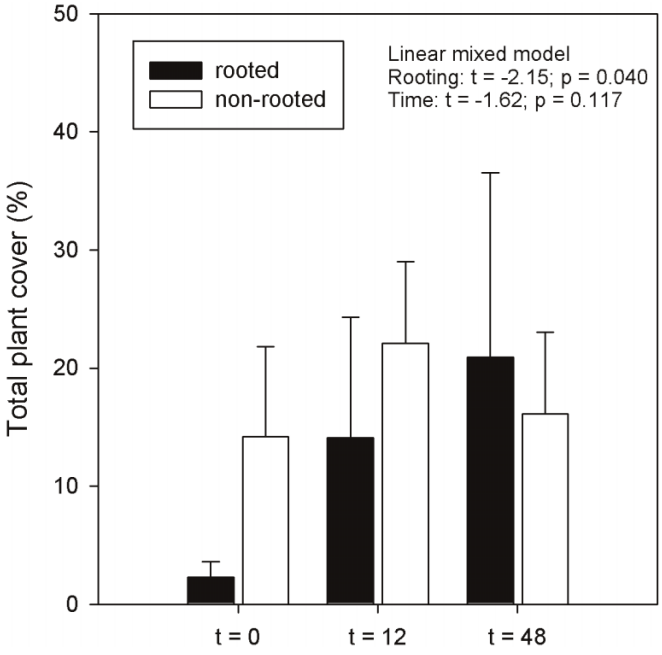


Fig. 3. Number of saplings measured on rooted and non-rooted plots at time = 0, 12, and 48 months, respectively (n = 6 for all graphs). Data represent averages ± SEs of sites.

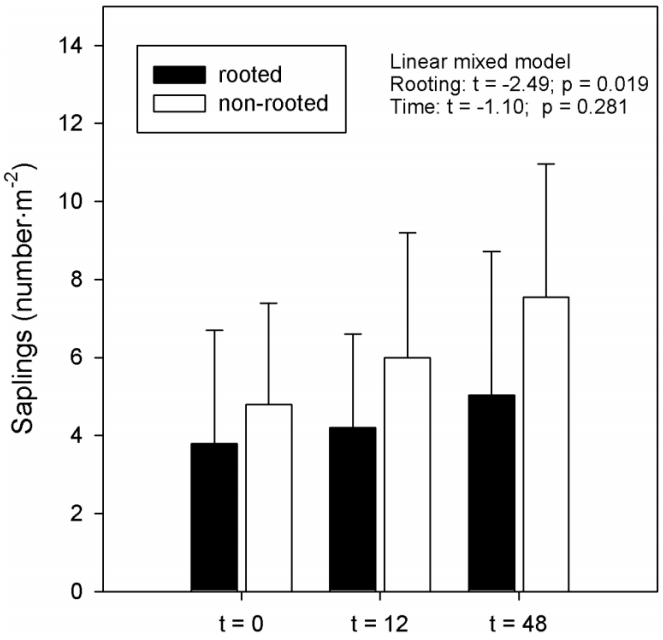
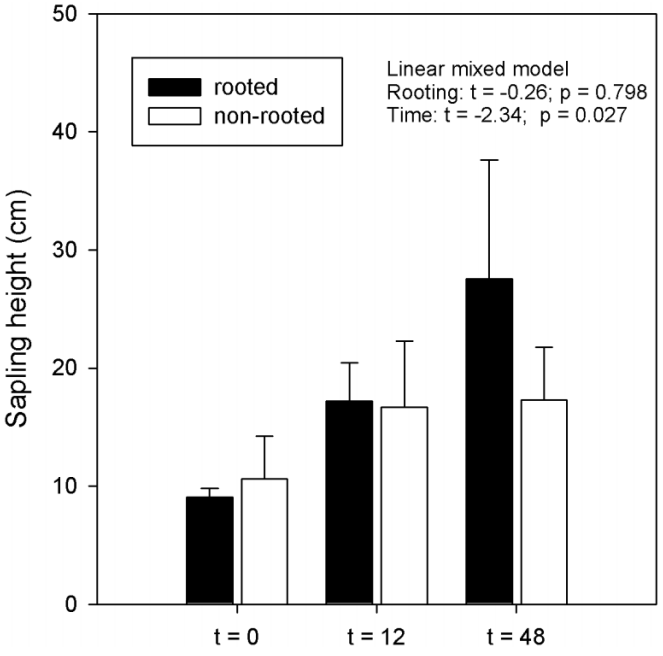
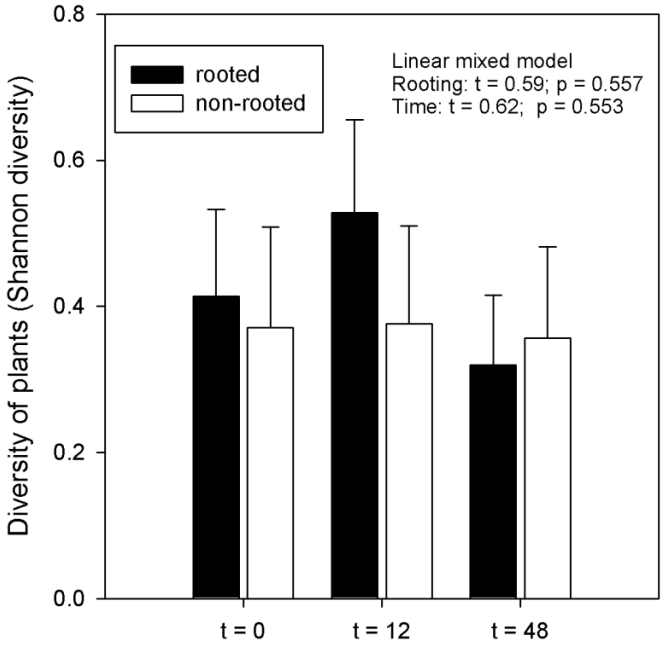


Fig. 4. Sapling heights measured on rooted and non-rooted plots at time = 0, 12, and 48 months, respectively (n = 6 for all graphs). Data represent averages ± SEs of sites.



derink and Hazebroek 1996; Moody and Jones 2000; Mohr et al. 2005), no differences in OM, C, and N concentrations were found between rooted and non-rooted plots. Given the higher turnover rates detected after boar rooting on our study sites, we were surprised that plant available N was not elevated but significantly lower on the rooted compared with the control plots. These results stand in contrast with findings by Singer et al. (1984) who reported higher nitrate-N and ammonium-N concentrations on rooted plots indicating alteration in N transformation processes in Great Smoky Mountains National Park. We can think of three potential explanations for the reduced N availability on the rooted compared with the non-rooted plots in our study, which we discuss below.

Fig. 5. Diversity of plants measured on rooted and non-rooted plots at time = 0, 12, and 48 months, respectively (n = 6 for all graphs). Data represent averages ± SEs of sites.



(*i*) *Nitrogen removal by plant uptake*. Increased N uptake, storage, or recycling by the vegetation could be responsible for the lower plant available N. Yet in our study, we did not detect higher plant growth; instead, total plant cover and the number of saplings were reduced on the rooted plots. Thus, alterations of understory N uptake likely cannot explain the lower availability of N. However, it is possible, as suggested by Singer et al. (1984), that N was taken up by tree roots and tree growth was accelerated on rooted plots, as shown by Lacki and Lancia (1986) who found greater shoot elongation of beech trees growing on rooted plots. Because we did not assess tree growth in our study, we cannot determine whether this mechanism would explain the lower N in our study.

(*ii*) *Immobilization by microorganisms*. It is possible that plant available N was immobilized by microorganisms on our rooted plots. Rooting by wild boars incorporates OM from the litter layer into the mineral soil (Groot Bruinderink and Hazebroek 1996), which increases resource availability (OM and C) and therefore favors the growth of the microbial communities. Since the C/N ratio of the incorporated OM is relatively high (typical for leaf litter), the soil microbes scavenge the soil solution to obtain enough N, which is required for the balance of nutrients (Homyak et al. 2008). Consequently, the increased microbial biomass found in our study could indicate that N was immobilized (incorporated into microbial cells), which resulted in depleted soil N (Marhan et al. 2010). In contrast with our results, investigations conducted in steep oak forests in Germany revealed lower microbial biomass on rooted compared with non-rooted loamy soils (0–5 cm) (Mohr and Topp 2001; Mohr et al. 2005).

These investigators found generally lower contents of organic C and total N in rooted plots compared with their control plots, which may explain the lower microbial biomass that they found at their rooted plots. We are not aware of any other study assessing the effect of wild boars on soil microbial biomass.

(*iii*) *Loss by leaching and erosion*. Nutrients may have been leached and lost from the soil. Since the understory vegetation, especially the herbaceous layer, is often reduced on heavily rooted soils (e.g., Bratton 1974, 1975; Siemann et al. 2009), which was also found in our study, nutrient uptake might be greatly reduced for some time after rooting (Singer et al. 1984). Thus, leaching of mineral N may be higher on rooted plots compared with plots with an intact herbaceous layer. In particular, due to their negative charge, nitrate ions are not adsorbed by the negatively charged colloids that dominate most soils (Gundersen et al. 2006). Therefore, nitrate ions move freely downward with drainage water and are readily leached. Moreover, by reducing soil bulk density, boar rooting may also accelerate soil erosion and therefore affect nutrient leaching directly. Supporting this idea, Mohr and Topp (2001) explained the decreases in organic C and total N of boar rooted soils in very steep oak stands as resulting from soil erosion and therefore loss of some of the freshly rooted material.

In addition to the impact on N availability, boars may influence understory vegetation directly by foraging (seed predation), uprooting, or mechanically damaging plants, therefore inhibiting certain plant species while favoring others. Yet, rooting had no effect on plant species diversity at our study sites. Several other studies found differences in plant species composition, but, with the exception of Welander (1995) and Ickes et al. (2001), they focused on the impact of feral pigs in forests where they have been introduced (e.g., Aplet et al. 1991; Peart and Patten 1992; Cuevas et al. 2010) or in grassland ecosystems (Kotanen 1995; Hone 2002; Cushman et al. 2004) (see Table 1). Where boars are an invasive species, they may affect the diversity and functioning of ecosystems differently than in systems where they are native (e.g., Siemann et al. 2009). Thus, one possibility for the highly variable outcome of boar rooting on plant species composition could be related to the intensity and frequency of rooting between the studies. Unfortunately, comparative data on intensity and frequency of rooting are not available. Another possible explanation for the variable results could be related to differences in the size of the plots used in the various studies (scale effects).

Overall, the net effect of disturbance by wild boars on understory vegetation in our study is complex and rather difficult to interpret. Yet, with the results of this present study, taking into account above- and belowground effects of rooting, we are able to depict a more complete picture of the role that boars play in forest ecosystems. Obviously, by rooting the soil, wild boars may enhance decomposition and accelerate turnover rates (mineralization) but, on the other hand, also diminish plant available N and reduce total plant cover and sapling counts. Thus, "friend-or-foe" thinking in wild boar/forest debates must be handled with care. Given that boars were shown to influence up to 53.8% of the forest soils within the larger surroundings of our study areas (Risch et al. 2010) and that the total area of Switzerland with more than 10 animals culled per 10 km^2 (numbers comparable with the numbers at our study sites) covered by hardwood or mixed hardwood forests amounts to 410 km^2 (Risch et al. 2010), we can assume that boars likely affect forest ecosystem functioning not only at the plot level but also at greater scales.

Consequently, this study contributes to the growing understanding of animal–plant, animal–soil, and plant–soil interactions in forest ecosystems, which can serve to address ecosystem stability/resilience, biodiversity, and sustainable management issues. This knowledge will be valuable given the potential increases in wild boar populations and habitat range predicted for Switzerland (Geisser and Reyer 2004) and other European countries.

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