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Wild-boar disturbance increases nutrient and C stores of geophytes in subalpine grasslands[1]

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- *Premise of the study:* Wild-boar soil disturbance (i.e., rooting) increases the abundance of some species of geophytes (i.e., plants with underground renewal buds) in upland meadows. However, the mechanisms that could lead to such enhanced prevalence remain unexplored.
- *Methods:* We analyzed the effects of wild-boar disturbance on the size, nutrient (N, P, K, C, and total ash), and nonstructural carbohydrate (soluble sugars, starch plus fructans, and total nonstructural carbohydrate) content of the storage organs of five taxa of upland geophytes. Results were explored in relation to the nutrient availability (total N, available P, and K) in the soil.
- *Key results:* Wild-boar rooting increased the size and the nutrient content of the storage organs of geophytes. Such enhanced storage was further promoted by rooting recurrence and intensity. Although we could not detect a direct impact of rooting on soil nutrient concentrations, plants were clearly N limited and such limitation was ameliorated in areas rooted by wild boar. Furthermore, plant-soil interactions for N were different in rooted areas, where plant N-concentrations responded positively to soil N.
- *Conclusions:* Geophytes growing in rooted areas have an increased nutrient value, which may promote the revisit of wild boars to previously rooted areas, with further positive feed-back effects on plant quality. This plant-animal interaction may shape upland geophyte communities.

Key words: Nitrogen; non-structural carbohydrates; phosphorus; potassium; Pyrenees; reserves; soil nutrients; storage organs; wild-boar rooting.

Disturbance is considered a main factor in the structure and dynamics of ecosystems, communities, and populations (Sousa, 1984; Grubb and White, 1985; White and Jentsch, 2001). This is due both to direct impacts on soil and vegetation, and to indirect effects through changes in the interactions and hierarchies among their biotic components (Sousa, 1984). The ultimate effect of disturbance, however, varies substantially depending on the type, timing, frequency, intensity or extent of the disturbance, and on the biotic and abiotic characteristics of the specific habitat where the disturbance is taking place (Sousa, 1984; Pickett and White, 1985).

Wild boar is one of the most widely distributed mammals worldwide (Oliver and Leus, 2008). Feeding practices of wild boar include rooting, i.e., turning over the soil looking for a large variety of underground feeding resources, generally at a depth from 5 to 15 cm (Barrios-García and Ballari, 2012) where most plant storage organs and soil invertebrates can be found (Brady and Weil, 2002). Wild-boar rooting is a major recurrent disturbance that affects large areas within wild-boar native and nonnative distribution-ranges (Massei and Genov, 2004; Oliver and Leus, 2008; Barrios-García and Ballari, 2012). Interestingly, this search for underground feeding resources is more intense in alpine and subalpine environments (Baubet, 1998; Baubet et al., 2004), where wild-boar rooting is considered a highly aggressive disturbance due to its relatively long-lasting effects and difficult recovery (Bueno et al., 2009). For example, in the Spanish Pyrenees, wild-boar rooting has been reported to affect up to 11% of subalpine grasslands where plant cover is completely removed, therefore deeply altering a vast extent of the available vegetation (Bueno et al., 2009). The effect of wild-boar rooting on the performance of some plant functional groups is not well-known, particularly with regards to geophytes (Sims, 2005). The main reason could be that geophytes are usually inconspicuous in summer, when floristic sampling is normally carried out in upland environments (Dafni et al., 1981).

Most ecological theories predict a low abundance of geophytes in soil-disturbed areas, while annual species seem to be better adapted to frequently disturbed environments (Grime et al., 1988; McIntyre et al., 1995). However, in subalpine grasslands, many geophytes are clearly favored by soil disturbances such as grizzly-bear digging (Tardiff and Stanford, 1998) or the digging by burrowing mammals like mole-voles (Borghi and Giannoni, 1997). For example, the density of *Merendera montana* (L.) Lange, an endemic geophyte of the Iberian mountains,

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was up to 44 times higher inside areas disturbed by mole-voles than in nearby undisturbed sites (Gómez-García et al., 2004). Vernal geophytes have indeed been suggested as indicative of seasonally recurrent disturbances (Hodgson et al., 2005). Similarly, in subalpine grasslands of the Pyrenees, areas rooted by wild boar are frequently covered by different species of geophytes which seem to be more abundant in disturbed areas than in nearby undisturbed soils (Bueno, 2011). One possible explanation is that, in subalpine grasslands, annual species are not very prominent (Bueno et al., 2011) probably due to the short vegetative period in these upland areas (Körner, 1999). In these grasslands, soil disturbance seems to favor species with vegetative propagation including many geophytes, although some species of upland geophytes are also negatively affected by wild-boar rooting (Bueno, 2011). Similar associations or *guilds* of plants promoted by animal disturbances have been described, for example, in tall-grass prairies disturbed by badgers, where plant-animal interactions shape plant communities and condition vegetation dynamics (Platt, 1975; Platt and Weis, 1977). Despite the prominent effect of wild-boar disturbances on vegetation, the mechanisms that could lead to an enhanced prevalence of some species of geophytes in subalpine grasslands disturbed by wild boar remain unexplored.

Soil disturbances caused by animals have been reported to produce a temporal increase in the availability of nutrients in alpine and subalpine soils. For example, either natural or simulated grizzly-bear digging was found to increase ammonium and nitrate availability in the soil of subalpine meadows in Glacier National Park, Montana, USA (Tardiff and Stanford, 1998). Similarly, wild-boar disturbances have been reported to cause an increase in soil nitrate availability in alpine and subalpine grasslands of the Pyrenees (Bueno, 2011; Bueno et al., 2013). Putative causes for such increase include reduced plant-nutrient uptake, increased aeration of soil organic matter and decreased nutrient immobilization by decomposers (Canals et al., 2003). If geophytes are able to survive, or even disperse, after the mechanical effect of wild-boar rooting, they may be able to benefit from the soil nutrients released after disturbance, since the resources accumulated in their storage organs enable them to grow faster than species regenerating exclusively from seed (Verboom et al., 2002). Indeed, soil disturbance seems to promote the asexual reproduction of some geophytes like *Merendera montana*, where the number of bulbs showing vegetative reproduction was up to 20 times higher in mole-vole disturbed than in undisturbed sites (Gómez-García et al., 2004). Geophytes may also be favored after soil disturbances by the lack of competition, by release of meristems due to mechanical disruption or by a combination of all the above (Kotanen, 1995; Cushman et al., 2004; Gómez-García et al., 2009).

If there is a positive effect of wild-boar rooting on the physiology of geophytes, these may show enhanced growth and may be able to provision larger amounts of stores in their reserve structures (bulbs, corms, tubers) after disturbance. This, in turn, may have potential consequences for the growth and reproduction of the following year(s) since the growth of geophytes strongly depends on the initial level of stores in the underground storage organs (Verboom et al., 2002; Werger and Huber, 2006). Also, in some species of geophytes it has been shown that reserves are positively related to the flowering success of plants in the following growth season (Tyler and Borchert, 2003). On the other side, the increased accumulation of nutrients in the storage organs of geophytes after disturbances may enhance their nutrient value. Similar to what happens with grizzly-bear digging (Tardiff and Stanford, 1998), such increased nutrient value could, among other factors (e.g., Bueno et al., 2009), encourage wild boars to revisit previously rooted areas, helping to explain the observed recurrence of wild-boar disturbance in certain sites (Welander, 2000). Despite the striking prevalence of geophytes in areas affected by wild-boar disturbances, no previous studies have analyzed the consequences of wild-boar rooting on the chemical composition of geophytes.

The aim of this study was to analyze the effects of wild-boar rooting on the nutrient and nonstructural carbohydrate content of the storage organs of geophytes in relation with the nutrient availability in the soil. We hypothesized that: i) wild-boar rooting will lead to enhanced nutrient and carbohydrate stores in the reserve organs of these plants; and ii) such increase will be further promoted by rooting intensity and related to the enhanced nutrient availability in rooted areas.

MATERIALS AND METHODS

Study plants and sites—We selected five taxa of geophytes for this study (Table 1) that produce their underground storage-organs within the soil-depth range commonly affected by wild-boar rooting. All of them are common and widely distributed in subalpine grasslands of the Spanish Pyrenees and show increased population numbers in areas rooted by wild boar. Also, similar to most plant species in the community, all study plants are phenologically active during spring and autumn, the main periods of wild-boar rooting in the study area (Bueno, 2011). According to the phytosociological classification (Braun-Blanquet, 1979), grasslands studied can be included in the *Bromion erecti* Koch alliance (hereafter BE), which covers the commonest subalpine pastures in the calcareous Pyrenees (Fillat et al., 2008). These plant communities comprise grasslands derived from upland forests that have been historically burned and cut for traditional grazing practices (Fillat et al., 2008).

Study populations of each taxon were selected after an extensive survey of the subalpine areas in the Western and Central Pyrenees frequently subjected to wild-boar disturbance and covered by communities of BE (Bueno, 2011). Due to interspecific differences in distribution, it was not possible to find all five study taxa growing together in each study site. Consequently, the number of study populations varied among taxa ranging from one to three (Table 1). The five sites selected covered the climatic and edaphic variability of BE communities in the Central and Western Pyrenees (Tables 1 and 2). In the study area, climate ranges from oromediterranean in the lowest and southern study areas (Punta Sora and Ordolés), to alpine in the highest site (Cuelloarenas), with higher precipitation and lower temperatures (Table 2). Lithology is mainly calcareous, from limestone to sandstone and conglomerates (Fillat et al., 2008). Soils range from neutral to slightly acidic (Table 2), being desaturated of bases and having high concentrations of organic matter and structural stability (Badía et al., 2002; Bueno, 2011).

Sampling design and plant harvest—Within each study site, we identified 5 (3 in the case of *Narcissus alpestris* Pugsley, *Crocus nudiflorus* Sm. and *Merendera montana*) areas recently disturbed by wild boar located more than 15 m apart from each other. Disturbed patches had an average surface of 220 m^2. They had been disturbed by wild boar recently (usually within the previous year), and were identified by the presence of overturned pieces of turf, which are characteristic of wild-boar rooting (Bueno et al., 2009). Samples from undisturbed patches were collected from areas surrounding each disturbance not affected by rooting and located at least 1 m away from the disturbance to avoid any potential border effect. These areas were completely covered by vegetation without any presence of overturned turf and forming a continuum with the surrounding grassland. Disturbances within the forest or in intensively grazed areas were avoided to preclude environmental variability. To account for the differences in intensity between disturbances, we measured (with a measuring tape) the maximum and minimum soil depth in each disturbed patch (in all study plants but *N. alpestris*) and calculated the average depth of the soil that was overturned by wild-boar rooting in each disturbance (Kotanen, 2004; Bueno, 2011).

Plant material was harvested at the end of the phenological cycle of each study plant, when most aboveground biomass (including fruits and leaves) was

TABLE 1. Taxa studied, study sites, and sampling dates.

Taxon	Taxonomic family	Date	Sampling sites	Elevation m a.s.l.	Geodesic coordinates
Asphodelus albus subsp. *delphinensis* (Gren. & Godr.) Díaz & Valdés	Liliaceae	21/7/2011	Punta Sora, Oroel	1.600	42°30′53”E 0°30′23”N
		22/7/2011	Ordolés, Oroel	1.270	42°30′21”E 0°30′54”N
		28/7/2011	La Trapa, Villanúa	1.820	42°41′29”E 0°28′34”N
Crocus nudiflorus Sm.	Iridaceae	5/7/2011	Aísa	1.800	42°45′45”E 0°35′35”N
Iris latifolia (Mill.) Voss	Iridaceae	19/8/2011	Aísa	1.800	42°45′45”E 0°35′35”N
		22/8/2011	La Trapa, Villanúa	1.820	42°41′29”E 0°28′34”N
		12/9/2011	Cuelloarenas, Ordesa	1.900	42°36′46”E 0°0′46”N
Merendera montana (L.) Lange	Liliaceae	17/7/2011	Cuelloarenas, Ordesa	1.900	42°36′46”E 0°0’46”N
Narcissus alpestris Pugsley	Liliaceae	20/6/2011	Cuelloarenas, Ordesa	1.900	42°36′46”E 0°0’46”N

senescent. At this phenological stage, plants are reduced to belowground organs and nutrient and carbohydrate reserves of geophytes are maximal yet quite stable (Rhizopoulou et al., 1997; Franková et al., 2003; Orthen and Wehrmeyer, 2004; Franková et al., 2006; Naor et al., 2008), allowing for interspecies comparison. In every sampling population, we collected a minimum of 6 individuals growing at least 1 m apart from each other, both inside and outside disturbances. Plant samples were kept cool in a portable cooler until reaching the laboratory. A composite sample of soil was obtained from inside and outside each disturbance by pooling subsamples collected from the soil surrounding every excavated plant.

Plant samples were taken to the laboratory immediately after harvest and stored at −20°C, until storage organs were separated from the leaves and fine roots. In the study plants, storage organs included bulbs, corms, and tubers. The number of storage organs in each sample was counted to account for individual organ weight. The fresh weight of each sample was obtained to calculate the water content (%). Samples were subsequently freeze-dried, weighed to the closest 0.01 mg and milled to a fine powder in a ball mill (Retsch Mixer MM301, Retsch U.K. Ltd., Leeds, UK). Soil samples were air-dried in the laboratory and sieved through a 2-mm mesh and ground finely before analyses.

***Chemical analyses*—**Total nitrogen (N) and carbon (C) mass-based concentrations were measured with an elemental analyzer (Elementar VarioMAX N/CM, Elementar Analysensysteme GmbH, Hanau, Germany). Subsamples were burned at 550°C for 4 h and ash was dissolved in HNO_3–HCl–H_2O (1:3:9) and filtered. Concentrations of potassium (K) in plant tissues were measured in the soluble (silica-free) ash by flame photometry and plant phosphorus (P) concentrations were assessed by vanado-molybdate colorimetry (Becker, 1961). Soluble sugars were extracted with 80% (v/v) ethanol/water and their concentration determined colorimetrically, using the phenol-sulphuric method of Dubois et al. (1956) as modified by Buysse and Merckx (1993). Starch and complex sugars remaining in the undissolved pellet after ethanol extractions were enzymatically reduced to glucose and analyzed as described in Palacio et al. (2007). Nonstructural carbohydrates measured after ethanol extraction are referred to as soluble sugars (SS) and carbohydrates measured after enzymatic digestion in glucose equivalents are referred to as starch. The concentration of total fructans was determined in one population per taxon by the Fructan HK kit of Megazyme (K-Fruchk 11/12, Megazyme International Ireland Ltd., Bray, Ireland) for the measurement of fructo-oligosaccharides and fructan polysaccharide. The sum of starch and fructan concentrations is referred to as nonstructural polysaccharides (NSP), while the sum of SS, starch, and fructans is referred to as total nonstructural carbohydrates (TNC).

Soil pH was measured in a 1:5 soil water suspension after shaking for 2 hours (Buurman et al., 1996). Total carbon, oxidizable carbon, and total nitrogen were analyzed with an elemental analyzer (Elementar VarioMAX N/CM, Elementar Analysensysteme GmbH) (Page, 1982). To quantify organic matter, oxidizable carbon content was multiplied by the Van Bemmelen factor (1.724). Available P was extracted with ammonium-fluoride (Bray and Kurtz, 1945), and measured colorimetrically at 430 nm (Page, 1982). Available K was extracted with ammonium-acetate (Page, 1982), and the concentration was determined by flame photometry. The carbon nitrogen (C:N) ratio was calculated by dividing the proportion of oxidizable carbon by the proportion of total nitrogen of each soil sample.

TABLE 2. Climatic and edaphic characteristics of study sites.

	Climate[a]		Soil				
Study sites	T (° C)	Pr (mm)	pH	SOM (%)	N (%)	P (%)	C:N
Punta Sora, Oroel	8.8	834.8	6.16	9.84	0.64	132.96	9.23
Ordolés, Oroel	9.4	815.5	7.06	7.01	0.41	134.87	9.91
La Trapa, Villanúa	7.0	1451.6	5.31	9.71	0.41	85.51	14.18
Aísa	6.4	1595.6	5.56	8.39	0.54	92.59	9.16
Cuelloarenas, Ordesa	5.0	1750.0	5.09	8.92	0.57	66.38	9.10

Notes: Abbreviations: T = Mean annual temperature; Pr = total annual rainfall; SOM = soil organic matter; N = nitrogen, P = phosphorus.

[a] Data obtained from the climatic atlas of Aragón (Gobierno de Aragón: http://anciles.aragon.es/AtlasClimatico/index.htm).

***Statistical analyses*—**The effect of wild-boar rooting on the size (average dry weight) and the N, P, K, total ash, SS, NSP and TNC concentrations and pools, and the C:N and N:P ratios of the storage organs of geophytes was explored by restricted maximum likelihood (REML) analysis, with “rooting,” i.e., sample from inside/outside rooted areas, as a fixed factor and “species,” “site,” and “replicate” (i.e., different rooted areas within a study site) as random factors (model 1). In the plants harvested from different sites (*Asphodelus albus* Mill. subsp. *delphinensis* (Gren. & Godr.) Díaz & Valdés and *Iris latifolia* (Mill.) Voss), inter-site variability was evaluated by REML analysis in each taxon separately, with “rooting” and “study site” as fixed factors and “replicate” as a random factor (model 2). The effect of the intensity of wild-boar disturbance on plant chemical composition was evaluated in samples collected inside disturbances by REML analysis with “average rooting depth” as a fixed factor and “species” and “site” as a random factor (model 3).

The effect of wild-boar rooting on nutrient availability in the soil was explored by REML models with “rooting”, i.e., sample from inside/outside rooted areas, as a fixed factor and “species,” “site,” and “replicate” (i.e., different rooted areas within a study site) as random factors with the N, P, and K concentrations in the soil as response variables (model 4). To evaluate the effect of the intensity of wild-boar rooting on soil-nutrient availability, soil N, P, and K concentrations inside disturbed areas were included as response variables in a REML model with “average rooting depth” as a continuous fixed factor and “species” and “site” as random factors (model 5). The effect of soil chemistry on the nutrient (N, P, and K) concentration of geophytes was analyzed by including soil N, P, and K concentrations, respectively, as a covariate in a

REML model with "rooting" as a fixed factor and "species," "site," and "replicate" as random factors (model 6). Finally, the potential effects of rooting intensity on the above relationship were explored by a REML model with nutrient (N, P, and K) concentration of geophytes collected inside rooted areas as response variables, "average rooting depth" as a fixed factor, soil N, P, and K concentrations, respectively, as a covariate and "species" as a random factor (model 7). Residuals were checked for normality and homogeneity of variances. When required, data were transformed to meet REML assumptions. Heterogeneous data were analyzed by including the varIdent structure in REML models (nmle package, Zuur et al., 2009). This structure allows for different variances among the different strata of the categorical factors included in mixed models (Zuur et al., 2009). All statistical analyses were run in R version 2.14.1 (R Core Team, 2012).

RESULTS

Effects of wild-boar rooting on the storage ability of geophytes—The storage organs of geophytes growing inside rooted areas were larger (Fig. 1, Appendix S1 - see Supplemental Data with the online version of this *a*rticle) and showed higher concentrations of C, N, and P (Fig.2), lower C:N ratios as well as higher N:P ratios and pools of N, P, (Figs. 1 and 2, Appendix S1 - see Supplemental Data with the online version of this article) and total C ($F_{1, 36}$ = 4.87, P = 0.034) than those growing outside wild-boar disturbances. Differences in nonstructural carbohydrate concentrations were only significant for nonstructural polysaccharides (NSP), i.e., the sum of starch and fructans which were higher in plants collected outside disturbed areas (Fig. 2). However, since the storage organs of geophytes growing inside wild-boar disturbances were larger, they accumulated more SS than plants growing in undisturbed sites, showing significantly larger pools (Fig. 1). We observed no significant differences in the water content (%) of geophytes growing in and out of disturbed areas ($F_{1, 33}$ = 0.72, P = 0.401), but differences among taxa were remarkable, with some taxa (*Asphodelus albus* subsp. *delphinensis*) holding up to 26% more water than others (*Crocus nudiflorus*; Appendix S1 - see

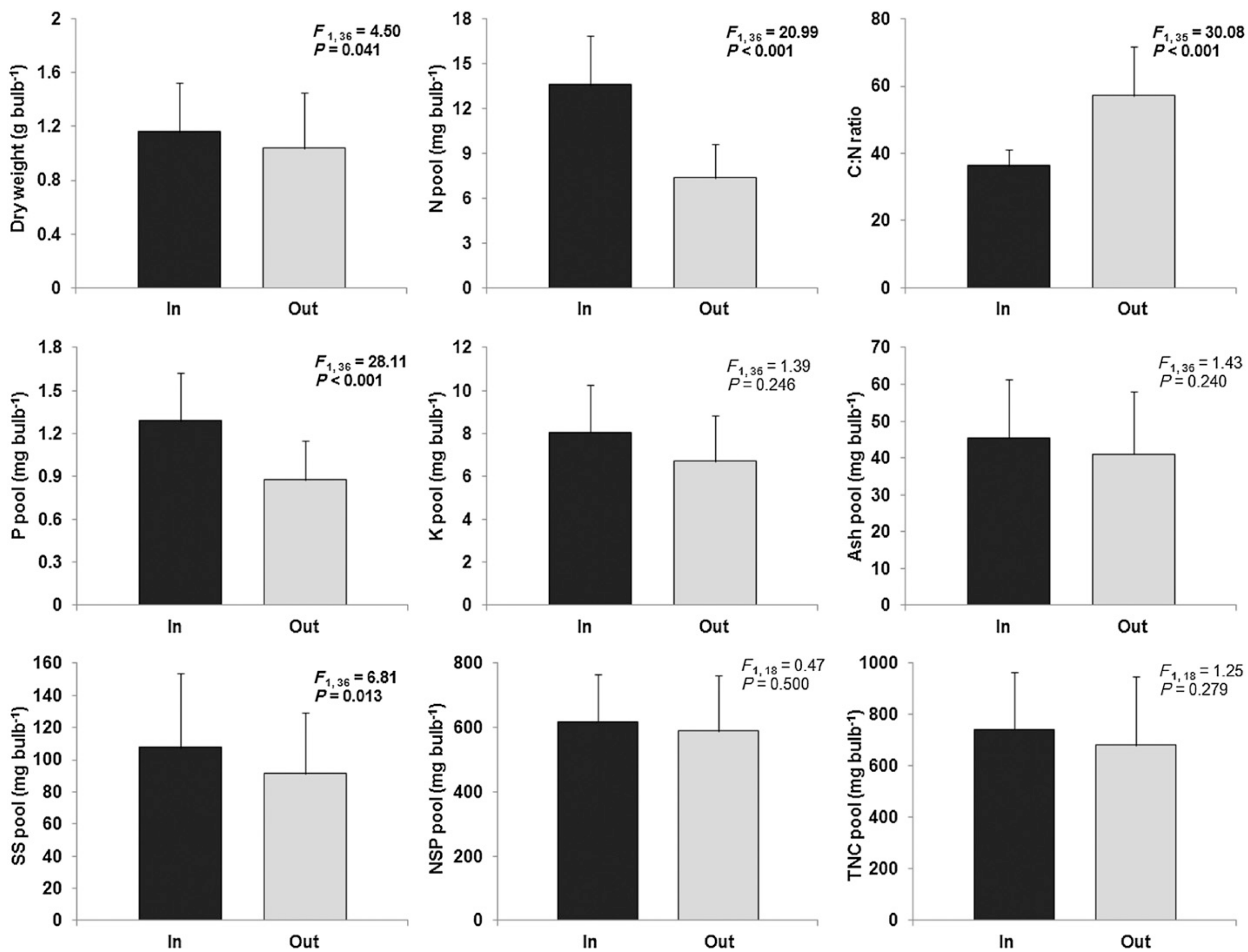

Fig. 1. Average dry weight, nitrogen (N), phosphorus (P), potassium (K), ash, soluble sugars (SS), nonstructural polysaccharides (NSP, sum of starch and fructans), and total nonstructural carbohydrate (TNC) pools (i.e., total amounts per plant) in the storage organs of study plants collected in (dark bars) areas and out (clear bars) of areas rooted by wild boar. Differences were assessed by using residual maximum likelihood (REML). The model (model 1) comprised wild-boar rooting as a fixed factor and taxon and plot as random factors. F-ratios$_{d.f.}$ are shown for the fixed factor along with P-values. Significant effects are highlighted in bold. Mean values across study plants are shown along with SE, n = 5.

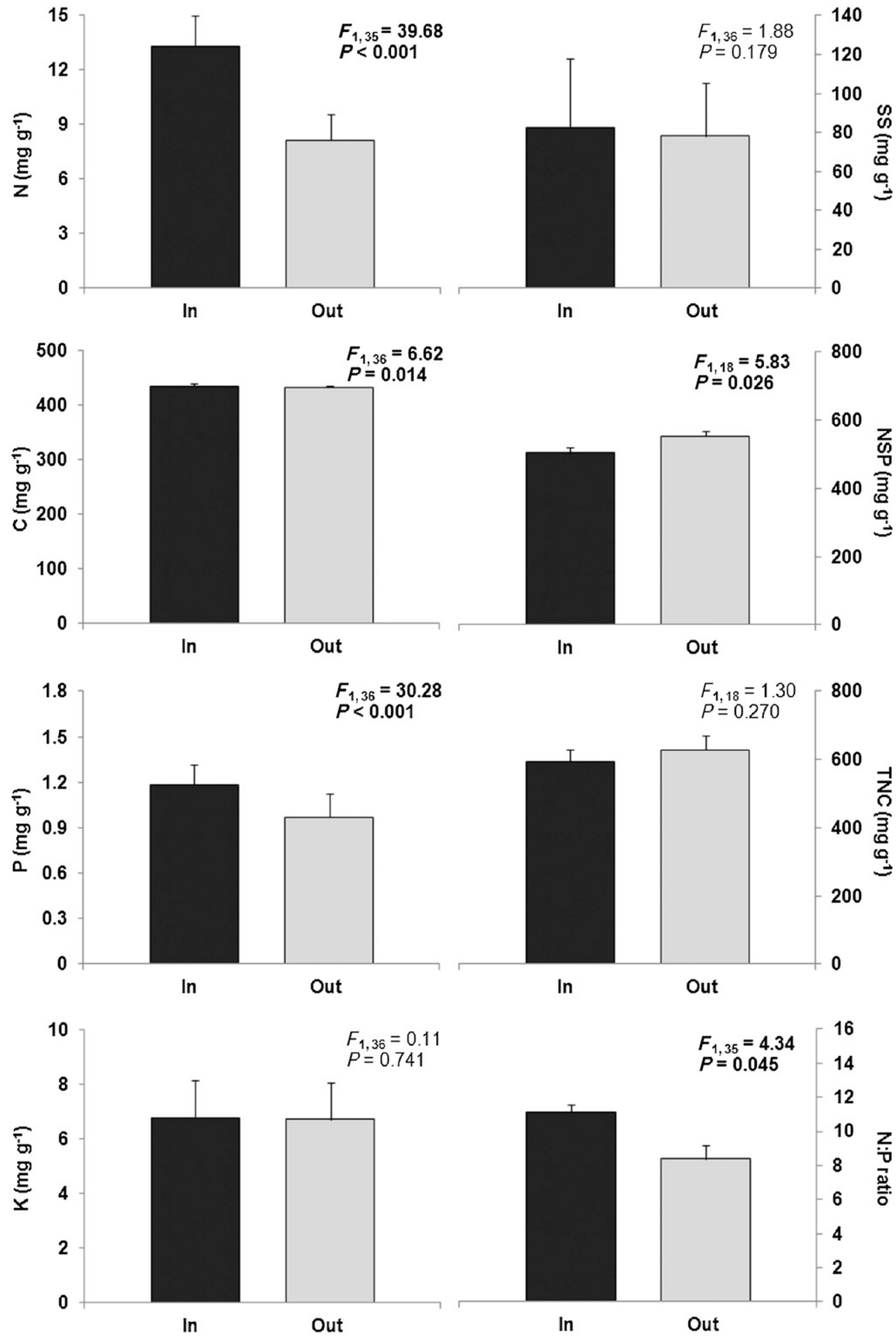

Fig. 2. Average nitrogen (N), carbon (C), phosphorus (P), potassium (K), soluble sugars (SS), nonstructural polysaccharides (NSP, sum of starch and fructans) and total nonstructural carbohydrate (TNC) concentrations, and N:P ratio in the storage organs of study plants collected in (dark bars) areas and out (clear bars) of areas rooted by wild boar. Differences were assessed by using residual maximum likelihood (REML). The model (model 2) comprised wild-boar rooting as a fixed factor, and study plant and plot as random factors. F-ratios$_{d.f.}$ are shown for each fixed effect along with P-values. Significant effects are highlighted in bold. Mean values across taxa are shown along with SE, n = 5.

Supplemental Data with the online version of this article). Finally, differences in the total mineral (ash) content of plants growing inside and outside rooted areas were not significant (Fig. 1).

Despite the fact that we could detect some spatial variability in the chemical composition of geophytes (Table 3), most of the differences described in the previous paragraph remained when different study sites were included in the REML models as fixed

TABLE 3. Results from restricted maximum likelihood (REML) analyses (Model 2, see methods section) on the effects of wild-boar rooting (in/out) and location of experimental sites on the size (dry weight) and chemical composition of reserve structures of the geophytes *Asphodelus albus* subsp. *delphinensis* and *Iris latifolia*. *F*-values are provided for n = 30 and d.f. = 1, 19 in *Asphodelus* and n = 26 and d.f. = 1, 15 in *Iris*. Significant effects (at $\alpha = 0.05$) are highlighted in bold where * *P*-values < 0.05, ** *P*-values < 0.01 and *** *P*-values < 0.001. Data for nonstructural polysaccharides (i.e., the sum of starch and fructans) and total nonstructural carbohydrate (including fructans) concentrations, and pools (i.e., total amounts per plant) were only available for one site per taxon and hence were not included in the analyses.

	Asphodelus albus subsp. *delphinensis*			*Iris latifolia*		
Response variable	Rooting (R)	Site (S)	R × S	Rooting (R)	Site (S)	R × S
Dry weight	2.31	2.81	0.57	2.57	0.612	0.78
Water content	0.76	0.04	3.10	0.05	1.55	**3.71***
N	3.83	**10.15****	0.40	**44.82*****	2.60	1.79
C	0.14	0.21	0.03	**16.27****	**7.38****	1.48
P	**8.35****	3.29	0.31	**9.43****	0.15	0.23
K	3.16	1.82	**6.32****	2.24	**36.43*****	1.25
Ash	0.86	0.08	0.53	2.17	**23.49*****	0.21
C:N	**7.41***	**9.98****	2.62	**30.70*****	**3.87***	0.75
N:P	0.40	**6.74****	0.66	**5.80***	0.74	0.09
SS	**5.52***	2.11	2.28	1.75	3.17	1.96
N pool	**9.06****	1.37	0.20	3.83	1.60	n.s.[a]
C pool	1.98	3.22	0.39	2.94	0.49	0.83
P pool	**7.37***	0.66	0.55	**8.54***	0.27	0.50
K pool	0.08	3.23	**4.70***	2.09	**5.44***	0.53
SS pool	**5.97***	**4.10***	1.16	1.06	1.42	1.51

Notes: Abbreviations: N = nitrogen, C = carbon, P = phosphorus, K = potassium, SS = soluble sugars.
[a] Interaction was not significant and led to collinearity issues (Zuur et al., 2009). Consequently it was excluded from the final model.

factors (analysis performed only for *Asphodelus albus* subsp. *delphinensis* and *Iris latifolia*, Table 3). Accordingly, rooting had a significant effect on the P and N concentrations and pools (marginally significant in the case of N) and the C:N ratio of both species (Table 3). The main exceptions were the dry weight and the C pools, which, contrary to the general results on all study plants together, were unaffected by wild-boar rooting in *A. albus* subsp. *delphinensis* and *I. latifolia* (Table 3). Also, rooting had a significant effect on the SS pools of *A albus*, but the effect was not significant in *I. latifolia*, while the opposite was true for the N:P ratio, which was only significantly affected by rooting in *I. latifolia* (Table 3).

The intensity of wild-boar rooting (measured as the average depth of the soil turned over by wild boar), had a significant impact on the N concentrations as well as the N, P, K, and ash pools of the storage organs of geophytes growing inside disturbed areas (Table 4). In all cases, increased intensity of rooting led to higher concentrations and pools of reserves in geophytes (Fig. 3). The P, K, SS, ash, NSP, and TNC concentrations, the C:N and N:P ($F_{1,18} = 0.49$, $P = 0.494$) ratios as well as the carbohydrate pools in the storage organs of geophytes were unaffected by rooting intensity (Table 4).

Impact of wild-boar rooting on soil nutrient availability and its relationship to the chemical composition of geophytes—We could not detect any direct effect of boar rooting on the N, P, and K concentrations of the soil (Table 5). Similarly, the intensity of wild-boar rooting did not change the nutrient availability in the soil at the time of sampling (Table 5). Nevertheless, the interaction between rooting and soil N had a significant effect on plant N-concentrations (Table 6) indicating an effect of wild-boar rooting on plant-soil interactions for N. Accordingly for plants growing inside rooted areas, the concentration of N in storage organs was positively related to N concentrations in the soil (Fig. 4), while such relationship was not significant for plants collected in undisturbed sites. Soil P-concentrations had a significant negative effect on plant P-concentrations when included as a covariate to "Rooting" or "Rooting intensity" in REML models (Table 6, Fig. 4). Finally, soil K-concentrations in areas disturbed by wild boar had a significant positive effect on the K concentrations of geophytes when included as a covariate to "Rooting intensity" in REML models, (Table 6).

DISCUSSION

Our results demonstrate that wild-boar rooting increases the size and the nutrient content of geophytes. These results generally stood despite the spatial variability across study sites. Interestingly, for plants growing in rooted areas, the positive effect of wild-boar rooting on the nutrient stores of geophytes was

TABLE 4. Summary statistics for restricted maximum likelihood (REML) analyses (Model 3) on the effect of rooting intensity on the chemical composition of storage organs growing inside areas disturbed by wild boar. Results for concentrations and pools (i.e., total amounts per plant) are displayed.

Response variable	d.f.	*F*	*P*-value	Response variable	d.f.	*F*	*P*-value
Dry weight	1, 19	4.15	0.056	**C:N**	1, 18	3.06	0.097
N	1, 18	**5.10**	**0.036**	**N pool**	1, 18	**12.82**	**0.002**
C	1, 19	0.79	0.385	**C pool**	1, 19	3.81	0.066
P	1, 19	4.13	0.056	**P pool**	1, 19	**7.92**	**0.011**
K	1, 19	3.04	0.098	**K pool**	1, 19	**10.10**	**0.005**
Ash	1, 19	1.77	0.200	**Ash pool**	1, 19	**11.29**	**0.003**
SS	1, 19	0.01	0.936	**SS pool**	1, 19	1.05	0.318
NSP	1, 11	0.02	0.879	**NSP pool**	1, 11	3.93	0.073
TNC	1, 11	0.01	0.997	**TNC pool**	1, 11	4.09	0.068

Notes: degrees of freedom (d.f.), *F*-values and *P*-values are provided. Significant effects (at $\alpha = 0.05$) are highlighted in bold. Abbreviations: N = nitrogen, C = carbon, P = phosphorus, K = potassium, SS = soluble sugars, NSP = nonstructural polysaccharides (i.e., the sum of starch and fructans), and TNC = total nonstructural carbohydrates (including fructans).

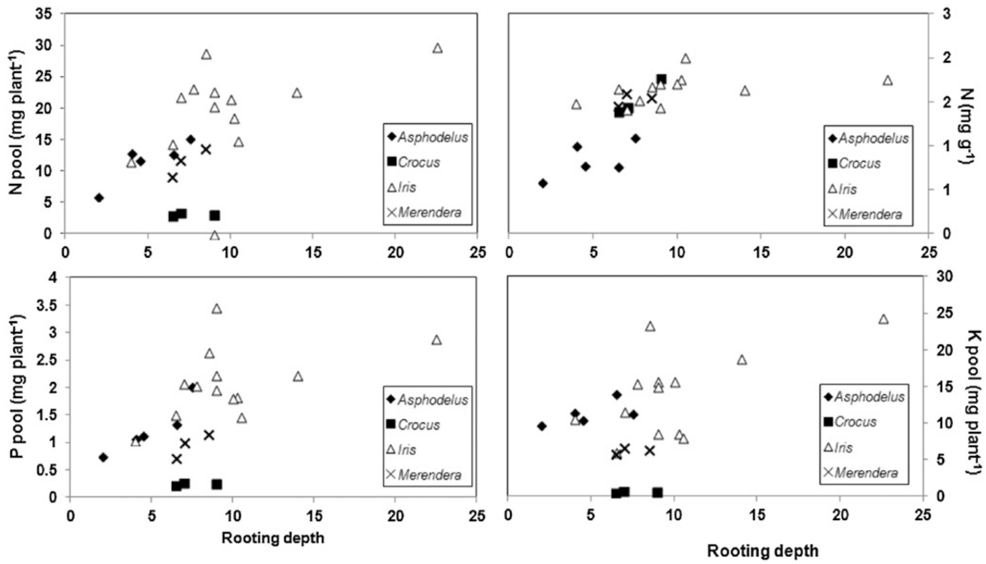

Fig. 3. Relationships between the intensity of wild-boar disturbances (rooting depth) and the chemical composition of the storage organs of geophytes growing inside rooted areas. Abbreviations as in Table 4.

clearly favored by rooting intensity. If we take into account that rooting depth is related to the recurrence of rooting disturbance (Kotanen, 2004; Bueno, 2011), our results indicate that repeated rooting by wild boar increases the nutrient content of the storage organs of surviving geophytes. Owing to the dependency of subsequent growth and, in some species, also reproductive success, on the amount of stored reserves in geophytes (Tyler and Borchert, 2003; Verboom et al., 2002; Werger and Huber, 2006), our results suggest that wild-boar disturbances favor the persistence of this type of plants in rooted areas, and that such effect is further enhanced by recurrent and/or more intense disturbances.

At least two mechanisms could explain the increased ability of geophytes to obtain resources in rooted areas, namely reduced competition of neighbors not surviving soil disturbance and increased availability of nutrients after soil disturbance (Tardiff and Stanford, 1998; Cushman et al., 2004). Both mechanisms may act simultaneously, for example, the combination of both increased fertility and reduced competition was related to larger underground storage-organs size and reserve provisioning after fire disturbance in the geophytic grass *Ehrharta capensis* Thunb. (Verboom et al., 2002). An increase in fertility due to wild-boar excrement must be rejected, taking into account the short time invested in digging and foraging by these animals (Bueno, 2011). Previous studies have demonstrated a temporal increase in nitrate and ammonium availability in mountain soils disturbed by wild boar (Singer et al., 1984; Lacki and Lancia, 1986; Bueno, 2011; Bueno et al., 2013). We could not detect a direct effect of wild-boar rooting or its intensity on the nutrient availability of soils. However, the N concentration of plants responded positively to soil N-availability only in rooted areas (Table 6, Fig. 4), indicating an effect of rooting on plant responses to soil N. Since soil sampling was conducted weeks after wild-boar rooting (i.e., time enough to allow plants to grow), we might have missed the initial pulse of soil N- availability after disturbance reported by previous studies. Nevertheless, our results show that the effects of rooting on soil-nutrient availability could be detected in plants. In the case of K and considering only rooted areas, our results indicate that concentrations of geophytes are in equilibrium with the K available in the soil, so that plants growing in richer soils show higher K concentrations. For available P, our results show a lack of correlation with soil N-availability (data not shown) and a negative relationship between soil and plant P-concentration, with plants growing in soils richer in P showing lower P-concentrations than plants from soils with lower P-availability. While these results seem hard to interpret, plants included in our study were more limited by N than P availability. Previous studies on the stoichiometry of plants indicate the N:P ratio is a reliable indicator of plant N- and P-limitation (Koerselman and Meuleman, 1996). For upland vegetation, N:P ratios lower than 14 seem to be indicative of N limitation, while N:P ratios above 14 would indicate P limits plant growth (Carline et al., 2005). The N:P ratio of plants from rooted areas was 11.2, while plants from undisturbed soils had an average N:P ratio of 8.4. Both values are clearly below 14, suggesting that plants included in this study were N-limited and that such N-limitation was reduced in areas disturbed by wild boar. Finally, reduced belowground plant competition after wild-boar rooting could also explain the increased ability of upland geophytes to secure nutrients. For example, increased exotic plant-taxa in coastal grasslands after feral-pig disturbance was found to be unrelated to changes in soil characteristics and reduced competition was suggested as the underlying mechanism (Cushman et al., 2004). Indirect wild-boar effects on the

Table 5. Wild-boar rooting effects on soil nitrogen (N), phosphorus (P), and potassium (K) concentrations after restricted maximum likelihood (REML) analysis with "rooting" or "rooting depth" as a fixed factor, and "species," "site," and "replicate," or "species" and "site" as random factors, respectively. The effects of rooting intensity were explored only on samples collected within disturbed areas.

Response variable	Rooting			Intensity		
	d.f.	*F* ratio	*P*-value	d.f.	*F* ratio	*P*-value
Soil N	1, 33	1.31	0.260	1, 19	1.05	0.319
Soil P	1, 33	0.02	0.901	1, 19	1.08	0.313
Soil K	1, 33	0.04	0.852	1, 19	0.42	0.525

TABLE 6. Results from restricted maximum likelihood (REML) analyses on the effects of wild-boar rooting (in/out, model 6), or its intensity (average depth, model 7), and the chemical composition of soils (N, P, and K concentrations) on the respective chemical composition of geophytes (N, P, and K concentrations). "Species," "site," and "replicate" were included as random effects in model 6, while only "species" was included as a random factor in model 7 (see text for further details on the analyses). Degrees of freedom (d.f.) and *F*-values are provided. Significant effects (at $\alpha = 0.05$) are highlighted in bold, where *P- values < 0.05, ***P*-values < 0.01 and ****P*-values < 0.001.

Response variable	Model 6					
	Rooting		Soil [a]		Rooting × Soil[a]	
	d.f.	*F*	d.f.	*F*	d.f	*F*
Plant N	1, 30	**33.80*** **	1, 30	0.00	1, 30	**4.60***
Plant P	1, 31	**27.22*** **	1, 31	**31.29*** **	1, 31	0.48
Plant K	1, 31	0.10	1, 31	0.95	1, 31	0.03
	Model 7					
	Intensity[b]		Soil [a]		Intensity × Soil[a]	
	d.f.	*F*	d.f.	*F*	d.f	*F*
Plant N	1, 16	**5.62***	1, 16	0.02	1, 16	0.31
Plant P	1, 17	**8.23***	1, 17	**21.07****	1, 17	**10.92****
Plant K	1, 17	2.19	1, 17	**11.76****	1, 17	2.14

[a] Corresponds to soil N, P, and K concentrations, respectively.

[b] Effects of the intensity of rooting were only explored on samples collected within disturbed sites.

nutrition of upland geophytes through reduced competition remain unexplored and hence cannot be ruled out.

In addition to the positive effects of rooting on the resource provisioning of geophytes, the prevalence of this type of plants in rooted areas can be due to an enhanced asexual reproduction after wild-boar disturbance (Kotanen, 1995). Some of the geophytes included in this study (like *Merendera montana*) are known to increase the frequency of vegetative reproduction in disturbed soils (Gómez-García et al., 2004). Although we did not record asexual reproduction in this study, we observed an increased frequency of bulblets in geophytes collected inside areas rooted by wild boar (S. Palacio, personal observation). Furthermore, the storage organs of plants growing inside rooted areas were much larger, and hence had a higher potential for vegetative reproduction, than plants from undisturbed patches. Such enhanced asexual reproduction could be due to a direct mechanical effect of wild-boar rooting through the fragmentation and propagation of propagules, as has been described in some species of *Crocus* (Mathew, 1982), but also to indirect effects through enhanced nutrient availability after rooting. Future research on the extent and mechanisms leading to such enhanced asexual reproduction is warranted.

Our results have important implications for the understanding of the recurrence of wild-boar rooting in upland areas. Among the putative mechanisms explaining the observed recurrence of wild-boar rooting are the closeness to water access, the enhanced ease of digging, and the higher frequency of desired plants in previously rooted areas (Bueno et al., 2009). Our results suggest that wild-boar rooting can also directly modify the nutrient value of geophytes, potentially making them more attractive for future wild-boar visits. Furthermore, the positive effect of rooting on the nutrient value of geophytes seems to be promoted by rooting intensity, so that recurrently rooted areas host the most nutritious plants of all. Similar results were

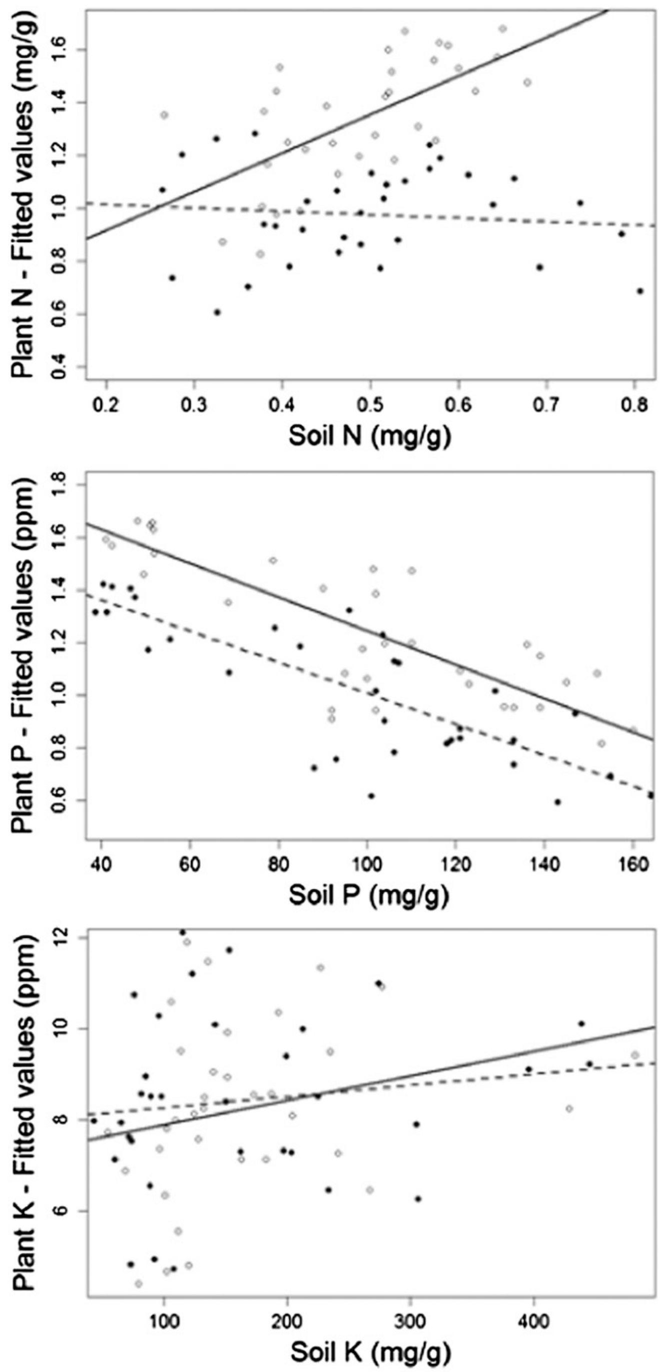

Fig. 4. Linear relationships between soil and plant concentration of nitrogen (N), phosphorus (P) and potassium (K) concentrations, collected from inside (black dots, solid line) and outside (white dots, dotted line) wild-boar disturbances, respectively. Plant concentration values correspond to fitted values from linear mixed models, with plant nutrient concentrations as response variables, soil concentrations, "rooting" occurrence, and its interaction as fixed factors, and "species," "site," and "replicate" as random effects (model 6). See Table 6 for further results on the models.

detected by Tardiff and Stanford (1998) on geophytes growing in areas disturbed by grizzly-bear digging. Nevertheless, although geophytes could make an excellent food resource for animals owing to their large amounts of nutrients and carbohydrates, many geophytes are also rich in alkaloids, tannins, and other secondary compounds, which make them toxic or unpalatable (Watt and Breyer-Brandwijk, 1962; Lovegrove and Jarvis, 1986). Most of the taxa included in this study belong to families known to accumulate important amounts of alkaloids and tannins. For example, *Merendera montana* contains several tropolonic alkaloids (Gómez-García et al., 2003, 2004) that can be lethal to cattle (Pijewska et al., 1967). Similarly, tubers of *Asphodelus aestivus* Brot., a close relative of *Asphodelus albus*, are rich in alkaloids and anthraquinones (Ghaleb et al., 1972) and several alkaloids have been identified in the bulbs of *Narcissus* species (Bastida et al., 2006). Such chemical compounds make consumption of these geophytes by wild boar unlikely. An alternative explanation to the observed relationship between wild-boar rooting intensity and the nutrient value of geophytes is that both groups of organisms benefit from the increase in soil-nutrient availability after disturbance. Owing to this explanation, wild-boar revisits to previously rooted areas would be encouraged by the higher presence of soil invertebrates and other underground organisms related to increased soil fertility (such as earthworms) (Baubet et al., 2004; C. G. Bueno and J. J. Jimenez, unpublished data). Wild boar may also indirectly benefit from the higher nutrient value of geophytes by consuming animals that feed on these plants. For example, mole-voles are able to peel the toxic envelope of *M. montana* bulbs and consume the rest (Gómez-García et al., 2004) and these animals are frequently predated by wild boar (Schley and Roper, 2003).

To conclude, our results demonstrate that geophytes growing inside areas rooted by wild boar have an enhanced ability to provision nutrient stores and that such enhanced storage is further promoted by rooting recurrence and intensity. Although we could not detect a direct effect of rooting in soil nutrient availability, plants were clearly N-limited and such limitation was ameliorated in areas rooted by wild boar. Furthermore, rooting changed plant-soil interactions for N, with plants from rooted areas responding positively to increased soil N-concentrations. Nevertheless, the potential positive effect of decreased plant competition on geophytes nutrition was not specifically assessed in this study and hence cannot be ruled out. The plant-animal interaction identified in this study helps to explain the observed prevalence of certain geophytes in areas rooted by wild boar, and may be at the basis of wild-boar effects on geophyte community composition and dynamics. Furthermore, our results have important implications for the understanding of rooting recurrence of wild boar as they indicate that geophytes growing in rooted areas could have an increased nutrient value, which may either directly or indirectly promote the revisit of wild boar to previously rooted areas, with further positive feedback effects on plant quality.

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