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Native and non-native ruderals experience similar plant–soil feedbacks and neighbor effects in a system where they coexist

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Abstract Recent applications of coexistence theory to plant invasions posit that non-natives establish in resident communities through either niche differences or traits conferring them with fitness advantages, the former being associated with coexistence and the latter with dominance and competitive exclusion. Plant–soil feedback is a mechanism that is known to explain both coexistence and dominance. In a system where natives and non-natives appear to coexist, we explored how plant–soil feedbacks affect the performance of nine native and nine non-native ruderal species—the prevalent life-history strategy among non-natives—when grown alone and with a phytometer. We also conducted field samplings to estimate the abundance of the 18 species, and related feedbacks to abundances. We found that groups of native and non-native ruderals displayed similar frequencies of negative, positive, and neutral feedbacks, resulting in no detectable differences between natives and non-natives. Likewise, the phytometer exerted comparable negative impacts on native and non-native plants, which were unchanged by plant–soil feedbacks. Finally, feedbacks explained plant abundances only after removing one influential species which exhibited strong positive feedbacks but low abundance. Importantly, however, four out of five species with negative feedbacks were rare in the field. These findings suggest that soil feedbacks and plant–plant interactions do not confer an advantage to non-native over native species, but do contribute to the observed coexistence of these groups in the system. By comparing natives and non-natives with overlapping abundances and strategies, our work broadens understanding of the consequences of plant–soil feedbacks in plant invasion and, more generally, coexistence within plant communities.

Keywords Central Argentina · Coexistence · Plant abundance · Plant–plant interactions · Plant–soil interactions

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Introduction

Like natives, non-native species must go through a series of abiotic and biotic filters to gain membership in local communities (Levine et al. 2004; MacDougall et al. 2009; HilleRisLambers et al. 2012). To dominate communities, however, non-natives must benefit from traits or conditions conferring them with advantages over the locals (Shea and Chesson 2002; Keane and Crawley 2002; MacDougall et al. 2009). Indeed, applications of current coexistence theory (Chesson 2000; Adler et al. 2007; Levine and HilleRisLambers 2009) to plant invasions suggest that non-native establishment occurs through either niche differences from the natives or traits and conditions favoring non-native over native fitness, but that non-native dominance

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is only reached through fitness advantage (MacDougall et al. 2009). Variations in spatial and/or temporal resource acquisition between these groups (Shea and Chesson 2002; Dukes 2002) and greater impacts of consumers on natives than non-natives (Keane and Crawley 2002; Mitchell and Power 2003) provide classical examples of niche and fitness differences, respectively. Within a community conceptual framework, assessing how natives and non-natives differ is thus crucial to understanding processes leading to the establishment and dominance of newcomers (Blaney and Kotanen 2001; Agrawal and Kotanen 2003; Suazo et al. 2012; Caplan and Yeakley 2013; Wainwright and Cleland 2013; Godoy and Levine 2014).

Plant–soil feedbacks are known to influence both the establishment and dominance of non-natives in resident plant communities (Wolfe and Klironomos 2005; Reinhart and Callaway 2006; Eppinga et al. 2006; Kulmatiski et al. 2008; van der Putten et al. 2013). In negative soil feedbacks, plants modify the biology and chemistry of soils in ways that limit the growth of their own species more than they limit that of other species (Bever et al. 1997; Kulmatiski et al. 2008); thus, negative feedbacks promote coexistence with the locals because pathogen loads eventually limit population expansion by the non-natives (Chesson 2000; Bever 2003; MacDougall et al. 2009; van der Putten et al. 2013). On the other hand, in positive soil feedbacks, non-native species benefit their own growth over that of the natives, and are consequently thought to trigger non-native dominance (Chesson 2000; Bever 2003; MacDougall et al. 2009; van der Putten et al. 2013). These benefits are thought to occur in at least two ways: the non-native plant facilitates soil microbial communities that are pathogenic to neighboring native plant species but not the non-native itself, or the non-native plant facilitates soil microbial communities that are beneficial to its own population expansion (e.g., symbiotic fungi enhancing resource uptake) but the neighboring native plants do not receive this benefit. In a pioneer study, Klironomos (2002) showed that five rare and endangered plants in Canadian old-field meadows exhibited strong negative soil feedbacks whereas, in sharp contrast, five non-native highly invasive species experienced neutral and positive feedbacks. Similarly, Perkins and Nowak (2013) reported that while three native grasses tended to produce negative plant–soil feedbacks, four non-native grasses tended to generate positive and neutral feedbacks in the Great Basin region of the United States. Although other work has not found differences in the direction of feedbacks between native and non-native plants, they have provided general support for the idea that soil feedbacks play a critical role in invasions, as natives generally experienced stronger negative feedbacks than non-natives (Agrawal et al. 2005; van Grunsven et al. 2007; Engelkes et al. 2008; MacDougall et al. 2011). These findings have, however,

been mainly reported from systems where non-native species are dominants. A recent analysis of the topic has concluded that the consequences of plant–soil feedbacks for invasions depend on the initial abundance of non-native species and how life-history traits of these species compare to those of natives, such that when non-natives are rare and exhibit life-history strategies similar to those of natives, soil feedbacks fail to promote non-native dominance (Suding et al. 2013). Comparing soil feedbacks in natives vs. non-natives in systems where they coexist may thus broaden our understanding of the importance of soil feedback for plant invasion and for structuring plant communities in general.

The soil feedback work described above was typically performed on single, isolated plants. However, in natural settings, soil feedbacks operate on interacting individuals; therefore, although that work is extremely valuable, it suffers from its simplified approach to modeling natural settings (Bever et al. 1997; Bever 2003; Eppinga et al. 2006; van der Putten et al. 2013). Interactions established with other members of the same trophic level are among the most pervasive (Tilman 1982; Chesson 2000; Adler et al. 2007; Callaway 2007), and they are likely to be influenced by plant–soil feedbacks (Bever 2003; van der Putten et al. 2013). Combined effects of plant–soil feedbacks and plant–plant interactions in the context of plant invasion have been addressed only recently (Eppinga et al. 2006; Reinhart and Callaway 2006; Shannon et al. 2010; Perkins and Nowak 2012), and examinations of how soil feedbacks affect plant–plant interactions in a group of native vs. non-native species are rare (Grman and Suding 2010; Meisner et al. 2013; Parepa et al. 2013).

Predicting how plant–soil feedbacks influence the outcome of plant–plant interactions can be difficult (Bever 2003; Casper and Castelli 2007; van der Putten et al. 2013). If feedbacks in plants growing alone translate directly to those growing with neighbors, then species with positive feedbacks will be less affected by competitive effects from neighbors than species experiencing strong negative feedbacks (van der Putten and Peters 1997; Reinhart and Callaway 2006; Petermann et al. 2008). Similarly, neutral feedbacks in isolated plants will not alter the interactions among those species when they are growing together (Bever 1994). Such direct connections may often, however, be absent (Bever et al. 1997; Bever 2003; Casper and Castelli 2007). Eppinga et al. (2006), for example, found that negative feedbacks generated by *Ammophila arenaria* can explain the invasive behavior of the species in non-native ranges because these feedbacks exert stronger negative effects on native plants than on itself, thus leading to a competitive advantage over the locals. Conversely, larger positive effects on a competitor than on itself may have negative consequences for the growth of a species (Bever et al. 1997; Bever 2003). That establishing predictions in this matter is not a straightforward task is well illustrated

by studies where expectations were not met by findings (Casper and Castelli 2007).

In the current work, we performed a large greenhouse experiment to explore how plant–soil feedbacks alter the performance of native and non-native species growing in isolation and with neighbors. In addition, we conducted extensive field samplings to estimate the abundances of the species used in the experiment, and related feedbacks to those abundances. We performed the study in the semi-arid open forest of caldén (*Prosopis caldenia*, Fabaceae) in central Argentina, commonly known as the Caldenal (Cano et al. 1980; Cabrera 1994). Similar to many natural systems around the world, most non-native invasive plants in the Caldenal are ruderals (sensu Grime 1974; Baker 1974; Mack et al. 2000; Hierro et al. 2005, 2006, 2011; Pearson et al. 2014a). Consequently, and in order to contrast native and non-native species with similar life-history strategies, we focused on comparing native vs. non-native ruderals. Native ruderals are also abundant and diverse in the Caldenal (Cano et al. 1980; Prieto 2000; Troiani and Steibel 2008), and recent plant surveys have revealed that 54 out of the 124 species recorded were ruderals native to the system (M.C. Chiuffo and J.L. Hierro, unpublished data).

Materials and methods

Study area

Plant–soil feedbacks were studied on native and non-native ruderal species that are common and co-occur in the Caldenal, a semi-arid open forest located in the southernmost portion of the Espinal province of central Argentina (Cabrera 1994). The forest understory contains shrubs (e.g., *Condalia microphylla*, *Schinus fasciculatus*, and *Lycium chilense*) and perennial bunchgrasses (e.g., *Piptochaetium napostaense*, *Poa ligularis*, and *Nassella* spp.). Virtually all natural grasslands in the Caldenal are grazed by domestic herbivores, mainly cattle, from around April to October (fall to spring in the Southern Hemisphere). Soils are sandy (Cano et al. 1980), mean annual precipitation is 638 mm, which mostly falls as rain in the spring and summer, and the mean annual temperature is 15.4 °C. Rainfall data cover the period 1911–2012 for Santa Rosa, La Pampa (36°35′30.86″S, 64°16′4598″W; G. Vergara, Agronomy Department, UNL-Pam, unpublished data), located at the heart of the Caldenal. Temperature data cover the period 1941–1990, again for Santa Rosa (http://www.worldclimate.com).

Field collection of soil and seeds

All soil feedback work included soils native to the Caldenal. Soil was collected in January 2010 from 10 randomly assigned natural grasslands located within a radius of 30–50 km around Santa Rosa. At each grassland site, ~2 kg of soil was collected from the top 0.10 m of several randomly located plots, pooled into a single sample, and thoroughly mixed. Upon collection, the soil was air dried for 7 days under ambient conditions in an area away from soil contaminants and stored at room temperature until it was used in the greenhouse experiment (see below) nearly 2 months later. Seeds of 18 ruderal species (nine natives and nine non-natives) were collected across the same grasslands in December 2009–January 2010. The selected native and non-native study species are generally common in the Caldenal (Troiani and Steibel 2008; Chiuffo and Hierro, unpublished data). Most non-native ruderals in this system were introduced as contaminants of agricultural species when the region was cultivated after being appropriated by the Argentinean government in 1879. The relatively recent and approximately simultaneous introduction of non-native species into the Caldenal suggests that time since introduction is not an explanatory factor for potential differences in plant–soil feedbacks among non-native species (Diez et al. 2010). Seeds were randomly collected from a minimum of five populations per species and, as with the soils, they were pooled into one sample for each species. Following the same protocols, seeds from the dominant native perennial grass *P. napostaense* were collected to use as a phytometer in order to test how plant–soil feedbacks affect the performance of ruderals when they grow alongside other plants (see below). *Piptochaetium napostaense* was chosen as a phytometer in this study because this grass is the most widespread and abundant plant species in the natural grasslands of the region (Cano et al. 1980; Rúgolo de Agrasar et al. 2005), it co-occurs with target ruderal plants, and it recruits and grows well after disturbance and under greenhouse conditions (Hierro et al. 2011).

Greenhouse experiment

The strength and direction (positive, neutral, or negative) of plant–soil feedbacks in the native and non-native ruderals when grown alone and with other species were assessed using a two-step plant–soil feedback experiment that included both intraspecific effects (species grown in soil trained by their own species) and interspecific effects (species grown in soils trained by heterospecifics; Bever et al. 1997). The experiment was conducted in a greenhouse at the University of Guelph, Canada, with average temperatures ranging between 23 and 17 °C (day/night) and a 16-h photoperiod. Plants were grown in 164-mL root-trainer pots, the depth of which (0.21 m) reduced constraints on vertical root development, including coiling (Annapurna et al. 2004). The pots were filled with a mixture of 20 % field soil, 55 % sand, and 25 % potting soil with no added

nutrients (Sunshine mix #2: sphagnum peat moss, coarse perlite, and dolomitic limestone). The top 0.02 m of the pots were filled with pure sand to prevent cross-contamination between pots. Prior to planting, seeds of all species were surface-sterilized with 2.5 % bleach for 10 min. The plants were arrayed on a greenhouse bench in a completely randomized design, and were watered with tap water as needed, but did not receive additional nutrients.

In the first step of the experiment, the soil mixture was trained with the different plant species by growing individual plants in 40 pots per species ($N = 18 \times 40 = 720$ pots) for 12 weeks (see Klironomos 2002; MacDougall et al. 2011). Pots were initially seeded with 10 seeds of each species, and emerging plants were thinned to a single healthy plant per pot after 2 weeks.

In the second step, all aboveground biomass was removed at 12 weeks by clipping, and the remaining soil mixture, including roots (trained soil), was used in the main part of the feedback experiment. Here, there were four treatments: (1) native and non-native ruderal species grown alone in their own soil to test the strength of feedback-based self-limitation; (2) native and non-native ruderal species grown alone in the soil of other species based strictly on origin (i.e., native species were only grown in soils of one of the nine non-natives, and vice versa) to test for heterospecific suppression based on soil feedbacks; (3) the same treatment as (1) but with one individual of *P. napostaense*; and (4) the same treatment as (2) but with one individual of *P. napostaense*. Under this design, the species used in the heterospecific treatments were assigned randomly and without replacement (e.g., MacDougall et al. 2011) from among the nine native or non-native species, given the impossibility of testing all possible pair-wise interactions with replication among the 18 species (i.e., $18! = 6.402E+15$). This approach of randomly assigning one species' soil as heterospecific soil to each target species is a weakness of this study, as the strength and direction of feedback effects (and differences among species both with and without a neighboring plant) depend not only upon the identity of the target species but also on the identity of the species providing the heterospecific soil. Also, this method did not allow us to specifically test the effects of one species on another (e.g., Bever et al. 1997), but it did serve as a community-level assessment of potential coexistence among co-occurring native and non-native ruderals in our system. There were 10 replicates for each of the treatments. The final sample size differed from the original due to some plant mortality (see the captions for Figs. 1 and 2). Also, pots in which *P. napostaense* did not germinate or survive were used as replicates of the species growing alone. As in the first step, the pots were initially seeded with 10 seeds of each ruderal species, and after approximately 2 weeks of growth the emerging plants were thinned to a single healthy plant. After another 12 weeks, the aboveground biomass of the ruderals
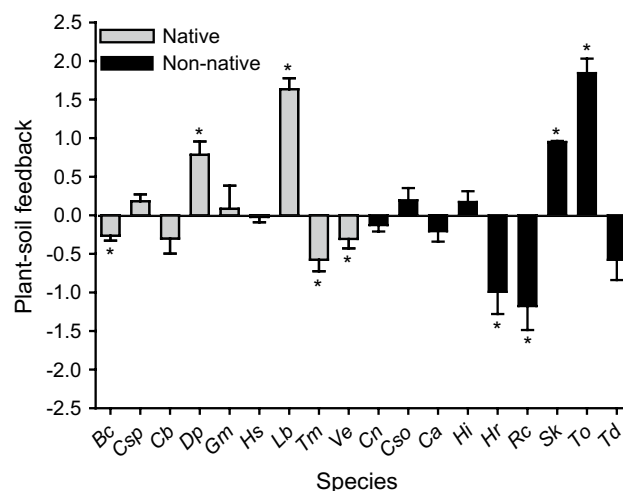
Fig. 1 Soil feedback responses of native and non-native ruderal species. *Bars* represent means + 1 SE. *Asterisks* show significant differences from zero plant soil feedbacks (i.e., no response) at $p < 0.05$ from *t* test. *Bc*, *Bromus catharticus* var. *rupestris* ($n = 13$); *Csp*, *Cenchrus spinifex* ($n = 11$); *Cb*, *Conyza bonariensis* ($n = 3$); *Dp*, *Daucus pusillus* ($n = 10$); *Gm*, *Gaillardia megapotamica* ($n = 8$); *Hs*, *Hordeum stenostachys* ($n = 15$); *Lb*, *Lepidium bonariense* ($n = 10$); *Tm*, *Thelesperma megapotamicum* ($n = 9$); *Ve*, *Verbesina encelioides* ($n = 7$); *Cn*, *Carduus nutans* ($n = 10$); *Cso*, *Centaurea solstitialis* ($n = 10$); *Ca*, *Chenopodium album* ($n = 9$); *Hi*, *Hirschfeldia incana* ($n = 6$); *Hr*, *Hypochaeris radicata* ($n = 9$); *Rc*, *Rumex crispus* ($n = 10$); *Sk*, *Salsola kali* ($n = 2$); *To*, *Taraxacum officinale* ($n = 14$); *Td*, *Tragopogon dubius* ($n = 11$)

was harvested, dried at 80 °C for 48 h, and weighed (Mackey and Neal 1993).

Field estimation of plant abundance

To estimate the abundances of our native and non-native species, field samplings were conducted at 30 randomly chosen natural grasslands (Online Resource 1 in the Electronic supplementary material, ESM). Vegetation was sampled as the percent cover of all species in five 1 m × 1 m plots per grassland site, separated by 50 m ($N = 30 \times 5 = 150$ plots). Samplings were conducted at the peak of flower/fruit production of target species (November–January; i.e., late spring to early summer). Species abundance was determined as the average cover of the species in all plots, not including plots where the species was absent (MacDougall et al. 2011).

Data analysis

Plant–soil feedbacks were calculated using the following equation (Petermann et al. 2008; Brinkman et al. 2010):

Plant-soil feedback = ln (Biomass conspecific soil/
    Biomass heterospecific soil).
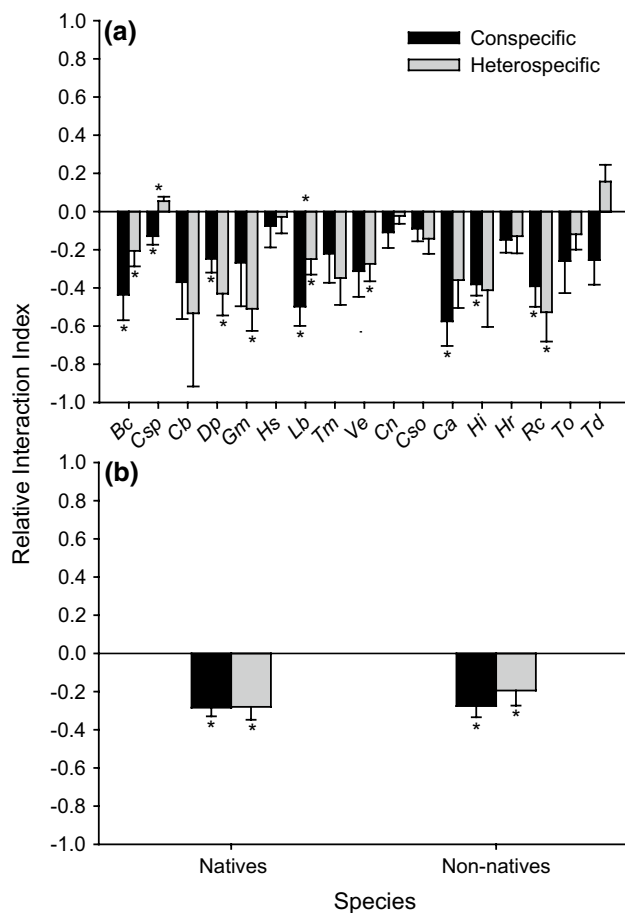
Fig. 2 Effects of the phytometer *Piptochaetium napostaense* on the aboveground biomasses of native and non-native ruderals, as quantified by the relative interaction index (RII). Target species were grown in soil trained by the same species (conspecific) vs. soil trained by other species (heterospecific): **a** individual species; **b** species grouped into natives and non-natives. *Bars* are means + 1 SE. *Asterisks above bars* indicate significant differences between soil pairs at $p < 0.05$ from *t*-test analysis; *asterisks below bars* indicate significant differences from zero RII (i.e., no phytometer effect) for individual conditioned soils at $p < 0.05$ from *t*-test. Species abbreviations are as in Fig. 1, and sample sizes are as follows: *Bc* ($n = 12$), *Csp* ($n = 14$), *Cb* ($n = 6$), *Dp* ($n = 15$), *Gm* ($n = 12$), *Hs* ($n = 12$), *Lb* ($n = 17$), *Tm* ($n = 10$), *Ve* ($n = 12$), *Cn* ($n = 16$), *Cso* ($n = 17$), *Ca* ($n = 12$), *Hi* ($n = 8$), *Hr* ($n = 14$), *Rc* ($n = 15$), *To* ($n = 16$), *Td* ($n = 10$)

This index provides negative values when a species performs better in soils of other species than in its own soil—a signature of intraspecific suppression, and positive values when a species does better in its own soils than those conditioned by another species.

Soil-feedback effects on native versus non-native ruderals were compared using a linear mixed model (LMM), where origin and species nested within origin were considered as fixed and random factors, respectively. In addition, *t*-tests were conducted to compare plant–soil feedbacks to zero (i.e., no feedback effect) for each group origin as a

whole and for each individual species. Group origin *t*-tests were conducted with the grand means of species within each group.

Quantifications of neighbor effects on the aboveground biomasses of native and non-native ruderals growing in both conspecific and heterospecific soils were performed using the relative interaction index (RII, Armas et al. 2004):

$$RII = (B_w - B_0) / (B_w + B_0),$$

where B_0 is the biomass of the target plant when growing alone and B_w is the biomass of the target plant when growing with other plants. The mean biomass of target plants in isolation was used for calculations. This index ranges from −1 to 1; it is negative for competitive interactions and positive for facilitative ones. Effects of ruderals on *P. napostaense* were not evaluated. *Salsola kali* had no recruitment in one of the treatments (heterospecific soil, growing with the phytometer), so it was not possible to calculate the index for this species.

Relative interaction indices were also analyzed with an LMM, where origin, soil (conspecific or heterospecific), and their interaction were considered fixed factors and species nested within origin was considered a random one. Additionally, differences in the effects of conspecific versus heterospecific soils on RII values of the individual species and how these values and those of native and non-native groups compare to zero were assessed with *t*-tests. Indices of *Conyza bonariensis* and *Lepidium bonariense* were log-transformed to meet *t*-test assumptions (Zar 2003).

Finally, the relationship between the strength and direction of plant–soil feedbacks was tested against the relative abundance of each species in the field using simple linear regressions. In the analyses, mean feedback for the species growing alone was used as the independent variable and its mean percent cover as the dependent one. For the analyses, percent cover of species found in no plot in the field was considered to be zero. Percent cover values are proportional data that are best analyzed using conventional models (i.e., models with normal errors and constant variance) following arcsine transformation (Crawley 2005). In addition, data points with Cook's distances greater than the recommended threshold of $4/(n - k - 1)$, where n is the number of observations and k is the number of explanatory variables (Cook 1977), were considered influential. If present, regressions were also run without them. Analyses were performed with IBM® SPSS® Statistics 20 (LMMs and *t*-tests) and Systat software® SigmaPlot 11.0 (regressions).

Results

The strength and direction of plant–soil feedbacks were species-specific rather than consistent within both native

Table 1 Biogeographic origin, life form, and percent cover (mean ± SD) of each of the 18 species used in this study

Species	Origin	Life form	Cover	Sample size
Bromus catharticus var. *rupestris*	Native	Annual grass	2.84 ± 2.63	18
Cenchrus spinifex	Native	Annual grass	5.51 ± 8.79	10
Conyza bonariensis	Native	Annual forb	3.92 ± 3.99	22
Daucus pusillus	Native	Annual forb	3.78 ± 2.45	4
Gaillardia megapotamica	Native	Perennial forb	2.68 ± 3.66	6
Hordeum stenostachys	Native	Perennial grass	7.50 ± 2.89	4
Lepidium bonariense	Native	Annual forb	15.00	1
Thelesperma megapotamicum	Native	Perennial forb	2.33 ± 2.31	3
Verbesina encelioides	Native	Annual forb	15.50 ± 20.51	2
Carduus nutans	Non-native	Annual forb	3.00 ± 2.31	4
Centaurea solstitialis	Non-native	Annual forb	10.00 ± 4.08	4
Chenopodium album	Non-native	Annual forb	18.41 ± 20.75	37
Hirschfeldia incana	Non-native	Annual forb	–	0
Hypochaeris radicata	Non-native	Perennial forb	–	0
Rumex crispus	Non-native	Perennial forb	–	0
Salsola kali	Non-native	Annual forb	18.77 ± 16.34	27
Taraxacum officinale	Non-native	Perennial forb	–	0
Tragopogon dubius	Non-native	Annual forb	–	0

Percent cover is the mean cover of the species in plots, excluding plots where the species was absent. *Sample size* is the number of plots in which a species was observed. Cover for species not observed in any plots is indicated by a *dash*

and non-native ruderal groups. Twenty-two percent of native species experienced positive, 44 % experienced neutral, and 33 % experienced negative feedbacks, and comparable responses were observed among the non-natives (Fig. 1; Online Resource 2 in the ESM). As a result, soil feedbacks in natives [0.135 ± 0.684 (mean ± SD)] and non-natives (0.009 ± 0.944) were similar ($F_{\text{origin 1, 16.187}} = 0.139$, $p = 0.714$) and did not differ from zero ($t_8 = 0.591$, $p = 0.571$ and $t_8 = 0.028$, $p = 0.978$, respectively).

In general, the phytometer *P. napostaense* exerted similar effects on target ruderal species when growing in conspecific vs. heterospecific soils (Fig. 2, Online Resource 3 in the ESM). Exceptions to this pattern were the natives *Cenchrus spinifex* and *L. bonariense*, for which impacts were less detrimental in heterospecific soils. Also, six native species experienced competitive effects from the phytometer when growing in at least one type of conditioned soils: *Bromus catharticus* var. *rupestris*, *Daucus pussilus*, and *L. bonariense* when growing in both conspecific and heterospecific soils, *Gaillardia megapotamica* and *Verbesina encelioides* when in heterospecific soils, and *C. spinifex* when growing in conspecific soils (Online Resource 4 in the ESM). In contrast, only three non-native species were negatively affected by the phytometer: *Rumex crispus* growing in both types of conditioned soils and *Chenopodium album* and *Hirschfeldia incana* growing in conspecific soils. As groups, however, both natives

(RII conspecific soil, $-0.284 ± 0.137$; heterospecific soil, $-0.280 ± 0.2018$) and non-natives (RII conspecific soil, $-0.276 ± 0.165$; heterospecific soil, $-0.1943 ± 0.224$) suffered comparable competitive effects (natives: conspecific, $t_8 = -6.229$, $p < 0.001$, heterospecific, $t_8 = -4.167$, $p = 0.003$; non-natives: conspecific, $t_7 = -4.692$, $p = 0.002$, -heterospecific, $t_7 = -2.455$, $p = 0.044$), regardless of the identity of the trained soil in which they were grown ($F_{\text{origin 1, 14.959}} = 0.209$, $p = 0.654$; $F_{\text{soil 1, 221.269}} = 1.729$, $p = 0.190$; $F_{\text{origin × soil 1, 221.269}} = 0.294$, $p = 0.588$).

Native and non-native study plants encompassed a wide range of plant cover in the field, which largely overlapped between groups (Table 1). Plant–soil feedbacks were positively related to plant cover only after removing one influential species, the non-native *Taraxacum officinale*, from the original data set ($r^2 = 0.091$, $F_{1, 16} = 1.600$, $p = 0.224$ vs. $r^2 = 0.358$, $F_{1, 15} = 8.354$, $p = 0.011$; Fig. 3). The influential species exhibited strong positive feedbacks but low abundances. Importantly, however, four out of the five species with negative feedbacks were rare in the field.

Discussion

To gain insight into the importance of plant–soil feedbacks for non-native plant invasion, our work addressed three main questions: how soil feedbacks of natives compare to
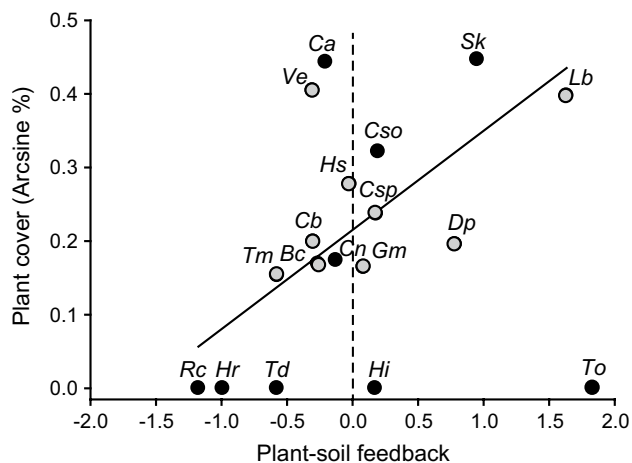
Fig. 3 Relationship between plant–soil feedback and plant cover for all species considered in this study. *Regression line* excludes data for *T. officinale*. *Circles*, which are *gray* for natives and *black* for non-natives, represent means. Species are indicated by *initials* (see Fig. 1)

those of non-natives, how soil feedbacks affect the performance of interacting native and non-native species, and how soil feedbacks relate to plant abundance in the field. Our study focused on native and non-native species sharing the ruderal strategy, which is the prevalent life-history strategy among non-native plants in our study area and globally (Baker 1974; Mack et al. 2000; Hierro et al. 2005). Our results showed that groups of native and non-native ruderals had similar frequencies of negative, positive, and neutral soil feedbacks, that native and non-natives suffered similar competitive effects, which were unaltered by soil feedbacks, and that most species that experienced strong negative feedbacks had low abundance in the field. Therefore, as predicted by coexistence and plant invasion theory (Bever et al. 1997; Chesson 2000; Shea and Chesson 2002; MacDougall et al. 2009; HilleRisLambers et al. 2012; van der Putten et al. 2013), these findings suggest that soil feedbacks and plant–plant interactions do not confer an advantage to non-native over native ruderals, but they do contribute to the observed coexistence of the groups in the semi-arid open forest of central Argentina.

The overlapping abundances of native and non-native species differentiate our study system from systems dominated by non-native plants, and from which predictions of soil feedbacks favoring non-natives over natives have often been derived (Klironomos 2002; MacDougall et al. 2011; Perkins and Nowak 2013). Recent modeling efforts have indicated that the expected promotion of non-native plant invasions by soil feedbacks does not occur when non-natives exhibit low abundance and life-history strategies are similar to those of natives (Suding et al. 2013), suggesting that both species groups are characterized by soil-feedback dynamics that curtail population expansion as plant

density increases. Our study offers experimental support for these conclusions, and shows that those expectations are similarly violated when the abundance of non-natives is comparable to that of natives. By comparing natives and non-natives with overlapping abundances and strategies, the current study broadens our understanding of the consequences of plant–soil feedbacks for plant invasion, and more generally, for coexistence within plant communities.

Given the worldwide importance of ruderals as non-native invaders (Baker 1974; Mack et al. 2000), other works have also investigated plant–soil feedbacks in ruderal species (Klironomos 2002; Callaway et al. 2004; Andonian and Hierro 2011; Andonian et al. 2011, 2012; MacDougall et al. 2011; Reinhart 2012), focusing in some instances on several of the same species studied here. Similar to our results, *Tragopogon dubius* was found to generate neutral feedbacks in semi-arid grasslands of North America (Reinhart 2012), and *Hypochaeris radicata* was found to generate negative feedbacks in an oak savannah of British Columbia in Canada (MacDougall et al. 2011). In contrast to our work, *Centaurea solstitialis* and *T. officinale* were both reported to establish negative feedbacks; the former across native and non-native distributions, including central Argentina (Andonian et al. 2011), and the latter in Canadian old-field meadows (Klironomos 2002). Variations in methodological protocols, such as the identity of the trainer of heterospecific soils (native grasses in Andonian et al. 2011 vs. native herbs in our study) in the case of *C. solstitialis*, and/or study systems (in the case of *T. officinale*), may help to explain the contrasting results between those studies and ours.

Effects from the dominant native grass *P. napostaense* on native and non-native ruderal species when growing in both conspecific and heterospecific soils were negative and also comparable between native and non-native groups. Double the number of native than non-native species, however, experienced competitive effects when growing in at least one type of conditioned soil. This result suggests that natives could be more susceptible to competition than non-natives, and deserves further investigation. Feedbacks observed for plants growing in isolation largely failed to predict the performance of those same species when grown with other plants. For example, the only two species displaying contrasting neighbor effects in conspecific vs. heterospecific conditioned soils offered counterintuitive results. *Cenchrus spinifex* generated neutral soil feedbacks in isolation; however, it was negatively affected by the phytometer when grown in its own cultivated soil. Similarly, as *L. bonariense* experienced positive soil feedbacks, neighbor effects were expected to be less negative (or more favorable) in conspecific than heterospecific soils; observations, however, indicated the opposite. These findings suggest that soil trained by both *C. spinifex* and *L.*

bonariense exerts stronger positive effects on *P. napostense* than on themselves, so they suffer competitive effects when growing with this species in their own trained soil (Bever et al. 1997; Bever 2003). Heterospecific soils may, in contrast, release them from these competitive effects. A deeper knowledge of plant–plant-soil interactions in our system is needed to understand these responses. In addition, using a phytometer to examine plant–soil feedbacks effects on plant–plant interactions limits the inferential scope of our study because these effects are commonly species-specific. Results reported here should consequently be considered as only an initial approximation to understanding how feedbacks affect plant–plant interactions in the ruderal community we examined.

Our study failed to document an unambiguous association between soil feedback and plant abundance, suggesting that factors other than soil feedback exert stronger control over the organization of native and non-native ruderal communities (Levine et al. 2006; Kulmatiski et al. 2011; Reinhart 2012; Harnden et al. 2013). Disturbance type and level, in terms of both frequency and intensity, are likely to be important determinants of the abundance and distribution of native and non-native ruderals in our system. Indeed, unreported vegetation analyses show that non-natives dominate ruderal communities in sites affected by strong disturbances, such as road maintenance (a combination of plowing and mowing, with no herbicide applications), whereas natives dominate communities growing in grasslands that have been recently burned (M.C. Chiuffo and J.L. Hierro, unpublished data). In the absence of strong disturbances, grasslands in the region generally offer remarkable resistance to non-native plant invasion (Hierro et al. 2006). Previous research has identified competitors (Hierro et al. 2011) and granivores (Pearson et al. 2014a, b) as major players in this resistance. These biotic interactions could explain the low abundance of *T. officinale* in spite of the strong positive feedbacks generated by the species, and more generally why species that experience positive feedbacks do not become dominant and exclude those suffering negative feedbacks in our system. The absence of plant–soil feedbacks that consistently favor non-native over native species may also contribute to the resistance of natural communities to invasion observed in the Caldenal. Future research should address how disturbance type interacts with soil feedback to influence native and non-native plant abundance (Carvalho et al. 2010; Veen et al. 2014). While much remains to be learnt, our study informs us that in a system rich in native species with a strategy similar to that of non-natives and where natives and non-natives display overlapping abundances, ruderal species established positive, neutral, and negative feedbacks in soils from natural grasslands regardless of species origin. Because feedbacks have scarcely been assessed in systems like ours, additional work is needed to test the generality of the findings reported here.

Author contribution statement MCC, ASM, and JLH conceived and designed the experiments. MCC performed the experiments. MCC and JLH analyzed the data. JLH, MCC, and ASM wrote the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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