

Response of native and non-native ruderals to natural and human disturbance

Mariana C. Chiuffo · Marina C. Cock · Aníbal O. Prina · José L. Hierro 

Received: 8 November 2017 / Accepted: 25 April 2018 / Published online: 28 April 2018
© Springer International Publishing AG, part of Springer Nature 2018

Abstract The ruderal strategy is widely shared among non-native plants, providing a general explanation for the commonly observed positive effects of disturbance on invasions. How native ruderals respond to disturbance and how their abundance compares to that of non-native ruderals remains, however, poorly understood. Similarly, little is known about the role that disturbance type plays in the coexistence between native and non-native ruderals. We proposed that natural disturbance favors native over non-native ruderals, whereas novel anthropogenic disturbance

favors non-natives over natives. To assess our general hypothesis, we conducted extensive field samplings in which we measured relative abundance, richness, and diversity of native and non-native ruderals in sites with natural and anthropogenic disturbance in central Argentina, a system where the ruderal strategy is common to a large number of native and non-native species. We found that natives dominated ruderal communities growing in recently burned grasslands, whereas non-natives dominated in roadsides. Additionally, the richness and diversity of native ruderal species were much greater than those of non-natives in sites with fire and in sites with grazing, but species richness and diversity did not differ between groups in roadsides. Because vegetation evolved with fire in our

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10530-018-1745-9>) contains supplementary material, which is available to authorized users.

M. C. Chiuffo · M. C. Cock · J. L. Hierro
Instituto de Ciencias de la Tierra y Ambientales de La Pampa, Consejo Nacional de Investigaciones Científicas y Técnicas-Universidad Nacional de La Pampa [INCITAP (CONICET-UNLPam)], Mendoza 109, 6300 Santa Rosa, La Pampa, Argentina

A. O. Prina
Facultad de Agronomía, UNLPam, Ruta 35 km 334, 6300 Santa Rosa, La Pampa, Argentina

J. L. Hierro (✉)
Facultad de Ciencias Exactas y Naturales, UNLPam, Av. Uruguay 151, 6300 Santa Rosa, La Pampa, Argentina
e-mail: jhierro@conicet.gov.ar

Present Address:

M. C. Chiuffo
Instituto de Investigaciones en Biodiversidad y Medioambiente [INBIOMA (CONICET-Universidad Nacional del Comahue)], Avenida de los Pioneros 2350, 8400 San Carlos de Bariloche, Río Negro, Argentina

system and, in contrast, the construction and maintenance of roads is recent in it, these results support our hypothesis. Our work indicates that the ruderal strategy does not seem to suffice to explain why disturbance facilitates invasions. According to our data, species origin interacts with disturbance type to determine dominance in communities with coexisting native and non-native ruderals.

Keywords Caldenal · Central Argentina · Coexistence · Distribution patterns · Plant abundance · Plant strategy

Introduction

Current plant communities around the world are typically composed of a mixture of both native and non-native species occurring at varying relative abundances (Mack et al. 2000; Simberloff et al. 2013; Chiuffo et al. 2015; Gross et al. 2015). Advances in community assembly theory posit that extant plant communities result from a number of biotic and environmental filters acting on a global pool of species that are dispersed by natural and human vectors (Lortie et al. 2004; HilleRisLambers et al. 2012). Species filters operate at both large biogeographical/regional scales and small local scales, with the latter affecting species coexistence (Chesson 2000; MacDougall et al. 2009; HilleRisLambers et al. 2012; Gallien and Carboni 2017). Within this conceptual framework, disturbance can be considered as a major selective agent, whose effects at large scales give rise to communities composed of native and non-native species with rapid growth, high fecundity, short life span, and high colonization ability, commonly referred to as weeds and technically to as ruderals (Grime 1974; hereafter definition of ruderal species adopted in this manuscript). Disturbance is also known to contribute to community assembly locally (Connell 1978; Sousa 1984; Pickett and White 1985; Dinnage 2009; García et al. 2016); however, how disturbance alters the relative abundance of natives versus non-natives in ruderal communities remains poorly investigated.

According to plant strategy theory (Grime 1974, 1977, 2001; Grime and Pierce 2012), ruderal species are expected to exhibit greater fitness (sensu Chesson 2000; Adler et al. 2007; MacDougall et al. 2009) than competitor and stress tolerant species when growing under disturbed environmental conditions, regardless of species origin. Non-native ruderals can be commonly overrepresented in datasets used to compare the response of native and non-native plant species to disturbance (Jauni et al. 2015), as the ruderal strategy is widely shared among non-native plants (Baker 1974; www.darwin.edu.ar, <https://plants.usda.gov>). Understanding dominance in current ruderal communities may then greatly benefit from comparing only native and non-native species sharing that strategy (Hierro et al. 2005; Caplan and Yeackley 2013; Chiuffo et al. 2015; Jauni et al. 2015). This approach can also contribute to uncover the importance of species origin in the invasion/colonization of disturbed sites (Davis et al. 2011; Simberloff et al. 2011). If origin matters, then native and non-native ruderals should respond differently to disturbance, but if origin does not matter, then both ruderal groups should perform similarly under disturbed conditions.

Disturbance type likely influences the relative abundance of native versus non-native ruderals. As early as 1879, Asa Gray proposed that non-native weeds are adapted to disturbance novel to natives, thus explaining the increased relative abundance of non-native plants in, for example, agricultural sites in North America (Baker 1974; Mack et al. 2000; Hierro et al. 2005). As a corollary, native ruderals should then dominate communities in sites altered by natural disturbance because of a shared evolutionary history with that type of disturbance. Some types of disturbance have been shown to exert stronger positive effects on the abundance of non-native plants than others (D'Antonio et al. 1999; Hierro et al. 2006; Jauni et al. 2015), but little is still known about the role that disturbance type plays in the coexistence between native and non-native ruderals.

The semi-arid open forest of *Prosopis caldenia* (Caldenal) in central Argentina exhibits a diverse composition of coexisting native and non-native ruderals (Cano et al. 1980; Prina 1995; Troiani and Steibel 2008; Chiuffo et al. 2015), whose abundance and distribution, like in many systems around the world, are controlled by several types of disturbance. Here, we took advantage of those features, and used

the Caldenal as a study system where to explore the effects of disturbance type on the abundance of native and non-native ruderals. We proposed that natural disturbance favors native over non-native ruderals, whereas novel anthropogenic disturbance favors non-natives over natives. We assessed our general hypothesis (Mahner and Bunge 1997; Marone and Galetto 2011) by conducting extensive field samplings, in which we estimated the cover of all plant species growing in sites affected by the main natural and anthropogenic disturbances in the system; that is, fire, grazing, and the construction and maintenance of roads. In addition, we classified species according to origin and strategy, and focused analyses on the performance of native versus non-native ruderals.

Materials and methods

Study area

Field sampling was conducted in the Caldenal of central Argentina. Biogeographically, the Caldenal is a district located in the southernmost portion of the Espinal province within the Neotropical region (Cabrera 1994). The forest understory is dominated by shrubs [e.g., *Condalia microphylla* Cav., *Schinus fasciculatus* (Griseb.) I. M. Johnston, and *Lycium chilense* Bertero] and perennial bunchgrasses [e.g., *Piptochaetium napostaense* (Speg.) Hack., *Poa ligularis* Steud., and *Nassella* spp.]. Soils are sandy (Cano et al. 1980), the mean annual temperature is 15.4 °C (1941–1990, Santa Rosa, La Pampa, 36°37'6.67"S, 64°17'29.31"W, located at the heart of the Caldenal, <http://www.worldclimate.com>), and the mean annual precipitation is 641 mm (1911–2015, Santa Rosa, G. Vergara, Agronomy Department, UNLPam, unpublished data), which mainly falls as rain in the spring and summer.

Ruderals and disturbance in the Caldenal

According to palynological records, native ruderal species, including members in the Brassicaceae and Asteraceae, were common in the vegetation of the Late Glacial-Holocene transition in the Caldenal (Prieto 2000). Non-native ruderals, in turn, were introduced to the region largely from Eurasia as contaminants of imported agricultural species after

1879; that is, when the Caldenal was made available for cultivation (Yunque 1957). The Caldenal is affected by several disturbance types of both natural and human origin, among which fire, grazing, and the construction and maintenance of roads dominate in extent (sensu Walker and Willig 1999; Fig. 1). Fire is the main natural disturbance in the Caldenal, and it occurs predominantly in the spring and summer (Medina 2007). Mean fire interval for the period 1911–1993 has been reported to be approximately 7 years (Medina et al. 2000). In addition, fire has historically been used by humans as a management tool in the system (Medina 2007; Medina et al. 2000). As for grazing, virtually all natural grasslands (i.e., grasslands composed of native vegetation) are grazed yearly by domestic herbivores from fall to spring in the Caldenal (Primer Inventario Nacional de Bosques Nativos 2006). Grazing by large mammals is not, however, novel to the Caldenal, as the system used to have a rich array of native herbivores that are now locally reduced or absent and extinct (Patterson and Pascual 1972; Bucher 1987). Also, physical and chemical defenses are common among native herbs and grasses in the Caldenal (Cabrera and Willink 1973). The other large disturbance in the system is the construction and maintenance of roads, which involves both the profound disruption of soil and extant vegetation and periodic plowing and mowing, with no herbicide application, on roadsides. Non-aboriginal settlement, mainly European immigrants, occurred only after 1879 in the study area (Yunque 1957), and road construction is a recent human practice in the Caldenal.

Vegetation sampling

To evaluate the response of native and non-native ruderal species to fire, grazing, and road construction and maintenance, extensive vegetation samplings were conducted during three consecutive years (2009–2012) at the peak of flower/fruit production of ruderal species (late spring to early summer) in the Caldenal. Since the Caldenal is affected by one of those disturbances in virtually all its distributional range (Primer Inventario Nacional de Bosques Nativos 2006), including “non-disturbance” sites in our samplings was not feasible. Only one natural reserve protects the Caldenal, but the area is grazed by a large



Fig. 1 Sites affected by the three main disturbance types in the *Prosopis caldenia* forest (Caldenal) of central Argentina. Burned grassland (a), grazed grassland (b), and roadside (c)

population of the European red deer (*Cervus elaphus*; Salomone 2005).

Only sites that burned in the spring–summer previous to the sampling (~ 1 year) were chosen for assessing the effects of fire on native and non-native ruderals. Upon finishing the main fire season in 2009, 2010, and 2011, the location of all occurred fires was obtained from the Civil Defense Office (<http://www.lapampa.gov.ar/defensa-civil.html>), a State dependency. The list included fire initiated both naturally (i.e., lightning) and accidentally (human-caused), and natural grasslands burned by lightning were chosen for sampling. From this list, burned sites were selected randomly under two conditions, sites had to be separated by at least 5 km between each other and a permit for sampling needed to be obtained from the land owner, as all fires occurred within private land. Along the 3-year-period, 19 burned natural grasslands were sampled (8 in 2009–2010, 6 in 2010–2011, 5 in 2011–2012). To minimize effects of confounding factors, such as soil type and topography, whenever possible (i.e., 16 burned sites), grazed natural grasslands and roadsides located at nearby/adjacent locations from burned grasslands were also sampled. In addition to those sites, other 14 grazed grasslands and 14 roadsides, also separated by at least 5 km between each other and randomly selected, were sampled (10 in 2009–2010, 12 in 2010–2011, 8 in 2011–2012 for grazed sites, and 12 in 2009–2010, 13 in 2010–2011, 5 in 2011–2012 for roadsides). In all cases, grazing and road construction and maintenance were sampled in nearby/adjacent sites. In roadsides, vegetation was sampled at approximately a mid-distance between the road and fence of private land, which was always a ranch. Collectively, sites were

spread across $394 \text{ km} \times 149 \text{ km}$ (5,870,600 ha, Fig. 2, Online Resource 1).

At each site, percent cover of vegetation, litter, and bare ground were visually estimated within five $1 \text{ m} \times 1 \text{ m}$ plots placed at 50 m intervals along a randomly located transect ($N = 79 \times 5 = 395$ plots). The sampling included the identification and visual estimation of percent cover of all species present in the plots. Plant cover was used to calculate ruderal species diversity with the Simpson's index, as $D = 1 - \sum p_i^2$ (McCune and Grace 2002), where p_i is the proportion of the cover of species i relative to the cover of all species combined. According to this index, plots with only one species have a diversity equals to zero. Plots with no ruderal species ($n = 27$) were not included into the analyses (e.g., Harte and Kitzes 2015). Plant species were classified according to biogeographical origin as natives or non-natives and plant strategy as ruderals or non-ruderals. For origin, the Southern cone catalog of vascular plants (<http://www.darwin.edu.ar/Proyectos/FloraArgentina/fa.htm>) was followed. For plant strategy, published information (Cano 1988; Prina 1995; Rúgolo de Agrasar et al. 2005; Troiani and Steibel 2008; Chiuffo 2016a, b; Fernández et al. 2016; Pissolito and Guerrido 2016), and personal observation were used as sources. Published information of species considered as ruderals or weeds are commonly available, given the economic importance of these species. Plant species that were not found in published sources were classified as ruderals only when they were observed in the field to exhibit traits included in the definition of ruderal adopted here.

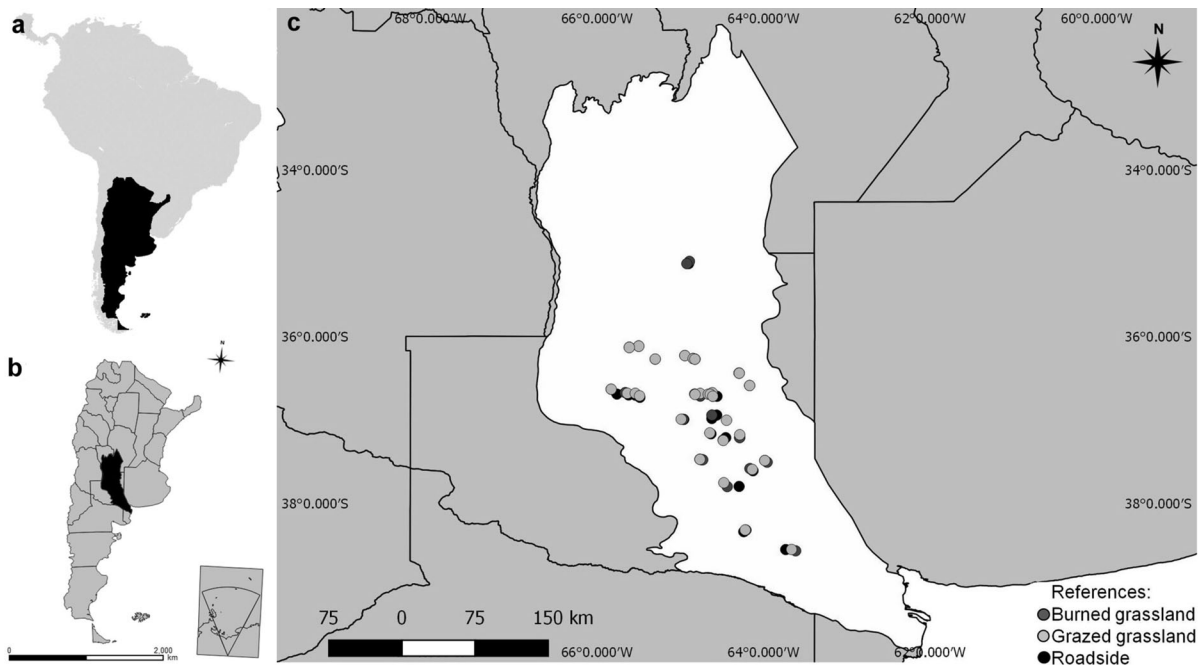


Fig. 2 Distribution of the 19 burned grasslands, 30 grazed grasslands, and 30 roadside sites sampled in this study during spring–summer 2009–2012 in the Caldenal of central Argentina. Panels depict South America map with Argentina in black (a),

Argentina map with the distribution of the Caldenal also in black (b), and the Caldenal with all 79 sample sites (c; not all sites are visible due to overlap)

Statistical analyses

Dependent variables were analyzed with Generalized Linear Mixed Models (GzLMMs) followed by pairwise comparisons corrected with sequential Bonferroni. In the model that compared the cover of ruderals, non-ruderals, litter, and bare ground between the different disturbances, disturbance type, group (i.e., ruderals, non-ruderals, litter, bare ground), and their interaction were considered as fixed factors and site as a random factor. In that comparing richness, diversity, and cover of native versus non-native ruderal species within and between disturbance types, species origin, disturbance type, and their interaction were considered as fixed factors and site as a random factor. In comparing the cover of native versus non-native ruderals, plots with no ruderal species were excluded from analyses ($n = 27$). Models used a binomial distribution and logit link function for cover, Poisson distribution and log link function for species richness, and a normal distribution and identity link function for diversity. In addition, differences in the composition of ruderal communities between disturbance types were assessed with detrended correspondence

analyses (DCA, Hill and Gauch 1980). The cover of each species in the 395 surveyed plots was used for this analysis. Values of the two first main axes were used to estimate the centroid and 95% confidence interval for each disturbance type. Communities growing in each disturbance type were considered as different when 95% confidence intervals did not overlap among each other in at least one of the ordination axis (Callaway et al. 2000; Cavieres and Badano 2009; Hierro and Cock 2013). Analyses were performed with IBM[®] SPSS[®] Statistics 22 (GzLMMs), PC-ORD (DCAs; McCune and Mefford 2011), and Sigma Plot[®] 11.0 (centroids and 95% confidence intervals; Systat Software, Inc. 2008).

Results

In total, 124 herb and grass species were recorded during field samplings; most of them native to the Caldenal (71%; Online Resource 2 and 3). In addition, 87 out of the 124 species exhibited a ruderal strategy, among which most were also native species (60%). Only one of the non-native species, *Sporobolus*

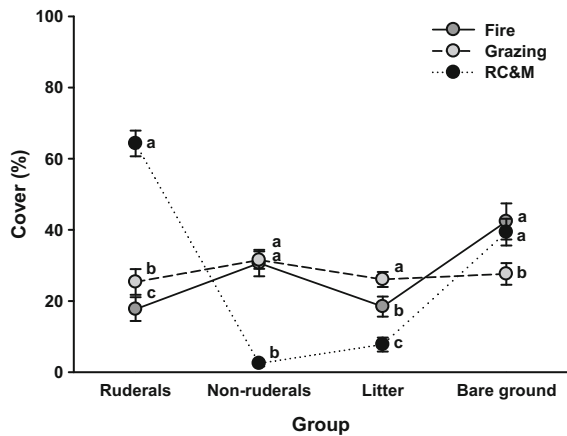


Fig. 3 Percent cover of ruderal species, non-ruderal species, litter, and bare ground in the different disturbance types studied here. Circles are means \pm 1 SE of 19, 30, and 30 sites with fire, grazing, and road construction and maintenance—RC&M—, respectively. Different letters indicate significant differences between disturbance types at $p < 0.05$

cryptandrus (Torr.) A. Gray, a perennial grass native to North America, did not belong to the ruderal strategy (Online Resource 4). All, but three, ruderal species found in our sampling were mentioned as belonging to that strategy in published sources.

The cover of ruderals, non-ruderals, litter, and bare ground varied according to the type of disturbance ($F_{\text{Disturbance } 2, 1568} = 2.347, p = 0.096$; $F_{\text{Group } 3, 1568} = 84.151, p < 0.001$; $F_{\text{Disturbance*Group } 6, 1568} = 117.978, p < 0.001$; Fig. 3). The cover of ruderals in roadsides was over two and three times greater than that in grazed and burned grasslands, respectively ($p < 0.001$ for both pair-wise comparisons). Ruderals were in addition more abundant in sites with grazing than in those with fire ($p = 0.013$). In contrast, the cover of non-ruderal species in grazed and burned sites was alike ($p = 0.616$), and 15 times larger in those types of disturbance than in road construction and maintenance ($p < 0.001$). Litter occupied a larger surface in grasslands disturbed by grazing than in the rest of the disturbance types ($p < 0.01$), and it was also larger in burned grasslands than in roadsides ($p < 0.001$). Finally, the cover of bare ground in sites altered by fire was similar to those altered by the construction and maintenance of roads ($p = 0.238$), and around 45% greater in those disturbance types than in grazing ($p < 0.001$).

The overall richness of native ruderal species was nearly 50% greater than that of non-native ruderals

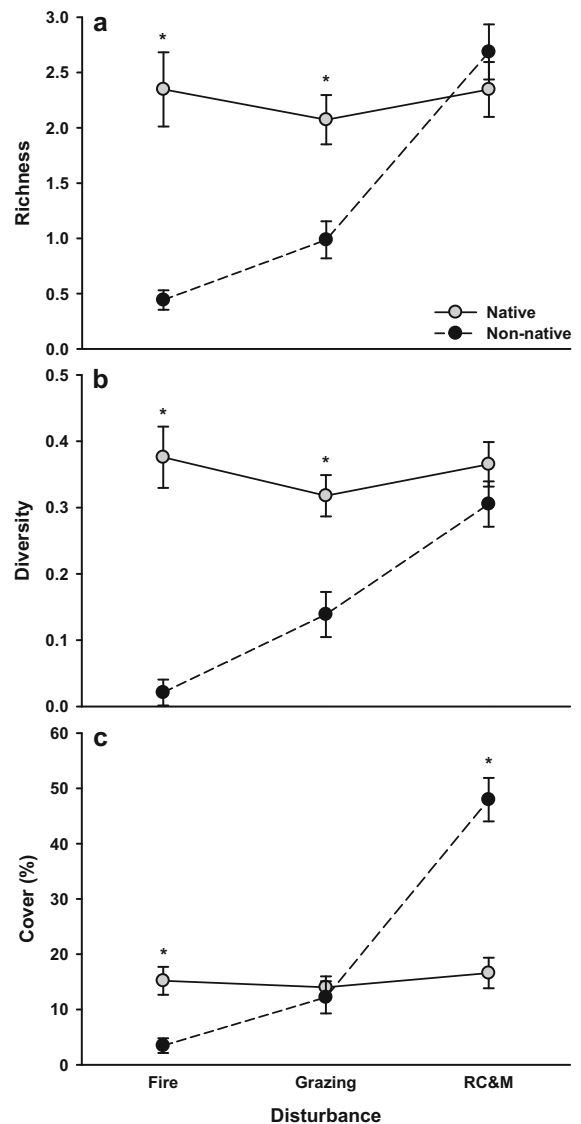


Fig. 4 Species richness (a), diversity (b), and cover (c) of native and non-native ruderals across disturbance type. Circles are means \pm 1 SE (richness, $n = 19, 30$, and 30 sites with fire, grazing, and road construction and maintenance—RC&M—, respectively; diversity, $n = 18$ and 15 sites with fire, $n = 30$ and 25 sites with grazing, and $n = 29$ and 30 sites with road construction and maintenance for natives and non-natives, respectively; cover, $n = 19, 30$, and 30 sites with fire, grazing, and road construction and maintenance, respectively). Asterisks indicate significant differences between species origins at $p < 0.05$

($F_{\text{Origin } 1, 784} = 118.924, p < 0.001$; $F_{\text{Disturbance } 2, 784} = 54.873, p < 0.001$; $F_{\text{Origin*Disturbance } 2, 784} = 60.580, p < 0.001$; Fig. 4a). In addition, sites affected by road construction and maintenance exhibited 64% and 80%

more ruderal species than those affected by grazing and fire, respectively ($p < 0.001$ for both pair-wise comparisons). Grazed grasslands were, in turn, 10% richer in ruderal species than burned grasslands ($p = 0.013$). Native ruderals exhibited two and five times more species than non-native ruderals in grazed and burned grasslands, respectively ($p < 0.001$ for both pair-wise comparisons; Fig. 4a), but natives and non-natives did not differ in species number in roadsides ($p = 0.066$). Interestingly, the richness of native ruderals did not vary across disturbance types ($p > 0.050$ for all pair-wise comparisons). That of non-natives was, instead, three and six times greater in roadsides than grazed and burned grassland sites, respectively ($p < 0.001$), and two times higher in sites with grazing than in sites with fire ($p < 0.001$). The diversity of ruderal species across disturbance types followed a pattern highly comparable to that of richness ($F_{\text{Origin } 1, 582} = 74.200$, $p < 0.001$; $F_{\text{Disturbance } 2, 582} = 15.684$, $p < 0.001$; $F_{\text{Origin*Disturbance } 2, 582} = 17.723$, $p < 0.001$; Fig. 4b).

In contrast to richness and diversity results, the overall cover of non-native ruderals was 55% larger than that of native ruderals ($F_{\text{Origin } 1, 730} = 4.286$, $p = 0.039$; $F_{\text{Disturbance } 2, 730} = 80.153$, $p < 0.001$; $F_{\text{Disturbance*Origin } 2, 730} = 95.179$, $p < 0.001$; Fig. 4c). Importantly, the cover of native ruderal species was over four times greater than that of non-natives in sites disturbed by fire ($p < 0.001$), but, in sharp contrast, the cover of non-native ruderals was nearly three times greater than the cover of natives in roadsides ($p < 0.001$). The cover of natives and non-natives did not differ in sites affected by grazing ($p = 0.080$). Similar to observations from ruderal richness and diversity, the cover of native species was highly comparable between disturbance types ($p > 0.500$), but that of non-native ruderals was nearly four times and over an order of magnitude larger in roadsides than in grazed and burned grasslands, respectively ($p < 0.001$). Non-native ruderals exhibited in addition over three times more cover in grazed than burned sites ($p = 0.001$). As expected from richness, diversity, and abundance results, DCA analyses showed that ruderal plant communities growing in sites altered by fire, grazing, and road construction and maintenance differed between each other in at least one of the ordination axes (Fig. 5).

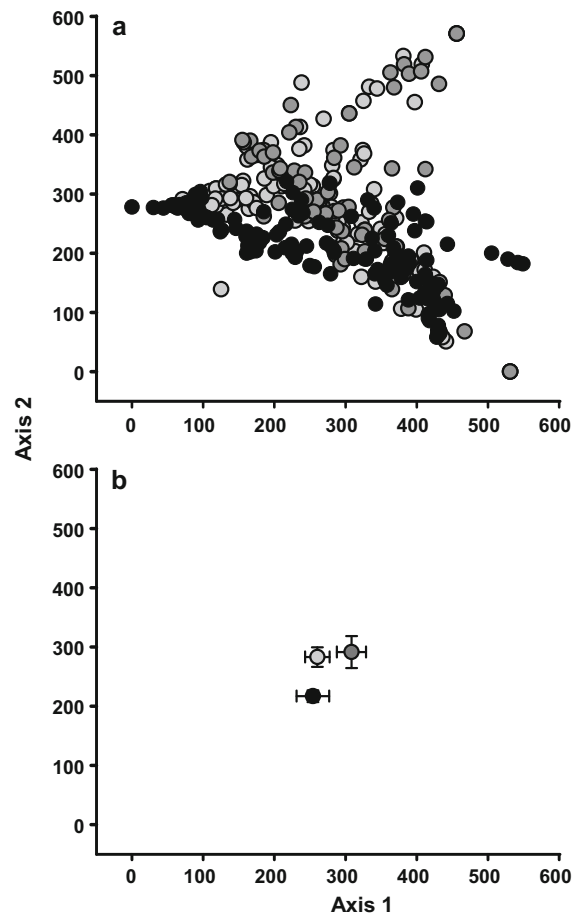


Fig. 5 Distribution of ordination scores for all ruderal species recorded in burned grasslands ($n = 95$, dark gray circles), grazed grasslands ($n = 150$, gray circles), and roadsides ($n = 150$, black circles), based on species cover (a), and means and 95% confidence intervals of the ordination scores for each disturbance type (b)

Discussion

The ruderal strategy is widely shared among non-native plants (Baker 1974), providing a general explanation for the commonly observed positive effects of disturbance on invasions (Mack et al. 2000; Hierro et al. 2006, 2011; Jauni et al. 2015, but see Moles et al. 2012). Here, we conducted extensive field samplings to assess the effects of different types of disturbance on the relative abundance, richness, and diversity of native and non-native ruderals in a system where the ruderal strategy is shared by a large number of native and non-native species. We found that natives dominated ruderal communities growing in

recently burned grasslands, whereas non-natives dominated in roadsides. Interestingly, differences in relative abundance between natives and non-natives within disturbance types arise from variations in the response of non-native ruderals to studied disturbances, as the abundance of native ruderals remained largely unchanged across disturbance types. In addition, the richness and diversity of native ruderal species were much greater than those of non-natives in sites affected by fire and in sites affected by grazing, but species richness and diversity did not differ between groups in roadsides. Because vegetation evolved with fire in the Caldenal (Medina 2007) and, in contrast, the construction and maintenance of roads is recent in the system, our results suggest that native ruderals are favored under conditions generated by the occurrence of natural disturbance, whereas non-native ruderals are favored under those created by novel anthropogenic disturbance, providing support to our hypothesis. Notably, non-natives achieved dominance of ruderal communities growing in sites altered by novel disturbance even though they were outnumbered in richness by native ruderals in the system. These findings are in line with early ideas (Gray 1879) about the importance of disturbance novelty in plant invasion. Additionally, our work indicates that the ruderal strategy does not seem to suffice to wholly explain why disturbance facilitates invasions. According to our data, species origin interacts with disturbance type to determine dominance in communities with coexisting native and non-native ruderals.

Comparing the response of native and non-native species with ruderal strategy to disturbance can provide fundamental insight into the role of disturbance in plant invasion (Moles et al. 2012; Jauni et al. 2015; Seabloom et al. 2015). According to a recent meta-analysis that did not group plant species into life-history strategies, disturbance, particularly human disturbance and grazing, strongly increases the diversity and abundance of non-natives, but disturbance does not affect those of natives (Jauni et al. 2015). In another study that similarly did not discriminate species by strategy, nutrient additions in global field experiments increased the cover and richness of non-natives, while additions decreased native diversity and cover (Seabloom et al. 2015). Contrasting responses of native and non-native plants to disturbance and nutrient additions were proposed to be due to an over-representation of the ruderal/opportunistic

strategy among non-native plants in both studies (Jauni et al. 2015; Seabloom et al. 2015). In our work, however, the strong response of non-natives to a severe human disturbance cannot be explained by differences in strategy with the natives because we controlled for plant strategy, highlighting the importance of species origin in the response (Davis et al. 2011; Simberloff et al. 2011; Richardson and Ricciardi 2013; Valéry et al. 2013; Simberloff and Vitale 2014). Similarly, origin seems to matter in the greater abundance of native than non-native ruderals observed in sites altered by a natural disturbance.

Experimental studies are needed to unravel mechanisms underlying documented patterns of ruderal plant distribution; here, we can only hypothesize about them. The alternative dominance of native and non-native ruderals may reflect a continuum of traits within species sharing the same life history strategy (Caplan and Yeackley 2013), with species dominating in burned natural grasslands at one extreme and those dominating in roadsides at the other. Because constructing and maintaining roads profoundly disrupt plant communities, including thoroughly removing extant vegetation, creating lower zones where water may accumulate, and periodically mowing and/or plowing, resource availability is likely to be higher at roadsides than at natural fields altered by fire and/or grazing. The scarce presence of non-ruderal vegetation and important cover of bare ground in roadsides detected in our study show the strong impact of road construction and maintenance on plant communities. Non-native ruderals in the Caldenal may possess adaptive traits that confer them an advantage over natives under the favorable environmental conditions presumably present at roadsides (Ordoñez et al. 2010; van Kleunen et al. 2011; Ordoñez and Olff 2013). In a greenhouse experiment that assessed trait differences between ten native and ten non-native ruderals in the Caldenal growing in isolation and under favorable conditions, the group of native species was, however, similar to that of non-natives for all study traits, including seed size, emergence rate, relative growth rate, height, time to flowering, aboveground biomass, and fecundity (Chiuffo 2016c). Thus, native ruderals in our system may also respond to high resource availability when growing in isolation. When in competition, however, natives may be outperformed by non-natives, which would explain the lack of response of native ruderals to roadside conditions.

Native ruderals, on the other hand, may be better adapted than non-natives to growing conditions in burned grasslands in the semi-arid Caldenal (Alpert et al. 2000). Our data show that the abundance of non-native ruderals was not only lower than that of native ruderals in burned grasslands, but it was also lower there than in roadsides, suggesting that non-natives perform poorly under the environmental conditions generated by fire and/or they are competitively outperformed by natives under those conditions.

Beyond adaptation and competition, other mechanisms could contribute to explain differences in abundance between native and non-native ruderals in sites with natural and novel human disturbance in our system. For example, the sign and magnitude of the feedbacks that native and non-natives establish with the soil may vary with disturbance type (Carvalho et al. 2010; Veen et al. 2014). Also, whereas biotic filters like granivores can be reduced or absent in roadsides (Pearson et al. 2014a), they can exert stronger control on non-native than native species in disturbed natural grasslands (Pearson et al. 2014b). Herbivores have been shown to facilitate non-native plant invasion (Orians 1986; Chaneton et al. 2002; Parker et al. 2006; Seabloom et al. 2009), and their exclusion has increased the cover of native plants, whereas caused no effects on non-native plants in a recent global field experiment (Seabloom et al. 2015). Descriptive surveys in our system have shown, however, that herbivory on native ruderals is similar to that on non-native ruderals across the disturbance types considered here (M.C. Chiuffo and J.L. Hierro, unpublished data). Finally, propagule pressure is commonly considered as a key driver of invasions (Lonsdale 1999; Loockwood et al. 2005), but the importance of this factor in setting dominance of natives versus non-natives in ruderal communities is currently unknown. Propagule pressure, on the other hand, can explain the greater abundance of non-native ruderals in roadsides as compared to natural disturbed grasslands (Harrison et al. 2002; Kalwij et al. 2008; Pauchard and Alaback 2004).

Despite limitations linked to the descriptive nature of our work, it advances the understanding of the importance of disturbance genesis in the assembly of current plant communities. By comparing native and non-native species sharing the same strategy, our study shows that disturbance type can alter the coexistence between native and non-natives in ruderal

communities, such that native ruderals dominate communities growing in sites disturbed by a natural disturbance, whereas non-native ruderals dominate those in sites affected by a severe human disturbance. Our approach highlights then that the effects of disturbance on the abundance of native and non-native ruderals may depend on both disturbance type and species biogeographical origin.

Acknowledgements We are grateful to land owners who facilitated the access to study sites. We also thank K. Echevarria for her assistance in the field and lab. This manuscript greatly benefited from the thorough revision and insightful comments of C. Alba and an anonymous reviewer. Funding for this research was provided by ANPCyT (PICT PIDRI 2007 0287), CONICET (PIP 114 201101 00206), and UNLPam (CN219) to J.L.H.

References

- Adler PB, HilleRisLambers J, Levine JM (2007) A niche for neutrality. *Ecol Lett* 10:95–104
- Alpert P, Bone E, Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspect Plant Ecol Evol Syst* 3:52–66
- Baker HG (1974) The evolution of weeds. *Annu Rev Ecol Evol Syst* 5:1–24
- Bucher EH (1987) Herbivory in arid and semi-arid regions of Argentina. *Rev Chil Hist Nat* 60:265–273
- Cabrera AL (1994) Regiones fitogeográficas argentinas. Primera reimpression. Acme, Buenos Aires (**in Spanish**)
- Cabrera AL, Willink A (1973) Biogeografía de América Latina. Serie Biología No: 13. OEA, Washington, DC (**in Spanish**)
- Callaway RM, Kikvidze Z, Kikodze D (2000) Facilitation by unpalatable weed may conserve plant diversity in over-grazed meadows in the Caucasus Mountains. *Oikos* 89:275–282
- Cano E (1988) Pastizales naturales de La Pampa, Tomo I. Convenio AACREA-Provincia de La Pampa, Buenos Aires (**in Spanish**)
- Cano E, Fernández B, Montes MA (1980) Inventario integrado de los recursos naturales de la provincia de La Pampa. UNLPam, Gobierno de la provincia de La Pampa e INTA, Buenos Aires (**in Spanish**)
- Caplan JS, Yeackley JA (2013) Functional morphology underlies performance differences among invasive and non-invasive ruderal *Rubus* species. *Oecologia* 173:363–374
- Carvalho LM, Antunes PM, Martins-Loucao MA, Klironomos JN (2010) Disturbance influences the outcome of plant–soil biota interactions in the invasive *Acacia longifolia* and in native species. *Oikos* 119:1172–1180
- Cavieres L, Badano E (2009) Do facilitative interactions increase species richness at the entire community level? *J Ecol* 97:1181–1191
- Chaneton E, Perelman SB, Omacini M, León RJ (2002) Grazing, environmental heterogeneity, and alien plant invasions in temperate Pampa grasslands. *Biol Invasions* 4:7–24

- Chesson P (2000) Mechanisms of maintenance of species diversity. *Annu Rev Ecol Evol Syst* 31:343–366
- Chiuffo MC (2016a) *Centaurea solstitialis* L. In: Herrera I, Goncalves E, Pauchard A, Bustamante RO (eds) Manual de plantas invasoras de Sudamérica. Trama Impresores, Santiago, pp 20–21 (in Spanish)
- Chiuffo MC (2016b) *Salsola kali* L. In: Herrera I, Goncalves E, Pauchard A, Bustamante RO (eds) Manual de plantas invasoras de Sudamérica. Trama Impresores, Santiago, pp 14–15 (in Spanish)
- Chiuffo MC (2016c) Ruderales exóticas versus ruderales nativas: respuesta a disturbios, retroalimentaciones planta-suelo y rasgos de historia de vida. Dissertation, University of Buenos Aires (in Spanish)
- Chiuffo MC, MacDougall A, Hierro JL (2015) Native and non-native ruderals experience similar plant–soil feedbacks and neighbor effects in a system where they coexist. *Oecologia* 179:843–852
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310
- D’Antonio CM, Dudley TL, Mack M (1999) Disturbance and biological invasions: direct effects and feedbacks. In: Walker LR (ed) Ecosystems of disturbed ground. Elsevier, Amsterdam, pp 413–452
- Davis MA et al (2011) Don’t judge species on their origins. *Nature* 474:153–154
- Dinnage R (2009) Disturbance alters the phylogenetic composition and structure of plant communities in an old field system. *PLoS ONE* 4:e7071
- Fernández OA, Leguizamón ES, Acciaresi HA, Troiani HO, Villamil CB (2016) Malezas e invasoras de la Argentina. Tomo II: descripción y reconocimiento, 1st edn. Universidad Nacional del Sur, Bahía Blanca (in Spanish)
- Gallien L, Carboni M (2017) The community ecology of invasive species: where are we and what’s next? *Ecography* 40:335–352
- García Y, Castellanos MC, Pausas JG (2016) Fires can benefit plants by disrupting antagonistic interactions. *Oecologia* 182:1165–1173
- Gray A (1879) The predominance and pertinacity of weeds. *Am J Sci Arts* 118:161–167
- Grime JP (1974) Vegetation classification by reference to strategies. *Nature* 250:26–31
- Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am Nat* 98:1169–1194
- Grime JP (2001) Plant strategies, vegetation processes, and ecosystem properties, 2nd edn. Wiley, New York
- Grime JP, Pierce S (2012) The evolutionary strategies that shape ecosystems. Wiley, Oxford
- Gross N, Liancourt P, Butters R, Duncan RP, Hulme PE (2015) Functional equivalence, competitive hierarchy and facilitation determine species coexistence in highly invaded grasslands. *New Phytol* 206:175–186
- Harrison S, Hon C, Ratay S (2002) Distribution of exotic plants along roads in a peninsular reserve. *Biol Invasions* 4:425–430
- Harte J, Kitzes J (2015) Inferring regional-scale species diversity from small-plot censuses. *PLoS ONE* 10(2):e0117527
- Hierro JL, Cock MC (2013) Herbivore-mediated facilitation alters composition and increases richness and diversity in ruderal communities. *Plant Ecol* 214:1287–1297
- Hierro JL, Maron JL, Callaway RM (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *J Ecol* 93:5–15
- Hierro JL, Villarreal D, Eren Ö, Graham J, Callaway RM (2006) Disturbance facilitates invasions: the effects are stronger abroad than at home. *Am Nat* 168:144–156
- Hierro JL, Lortie CJ, Villarreal D, Estanga-Mollica ME, Callaway RM (2011) Resistance to *Centaurea solstitialis* from annual and perennial grasses in California and Argentina. *Biol Invasions* 13:2249–2259
- Hill MO, Gauch HG Jr (1980) Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42:47–58
- HilleRisLambers J, Adler PB, Harpole WS, Levine JM, Mayfield MM (2012) Rethinking community assembly through the lens of coexistence theory. *Annu Rev Ecol Evol Syst* 43:227–248
- Jauni M, Gripenberg S, Ramula S (2015) Non-native plant species benefit from disturbance: a meta-analysis. *Oikos* 124:122–129
- Kalwij JM, Milton SJ, McGeoch MA (2008) Road verges as invasion corridors? A spatial hierarchical test in an arid ecosystem. *Landscape Ecol* 23:439–451
- Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* 80:1522–1536
- Loockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. *Trends Ecol Evol* 20:223–228
- Lortie CJ, Brooker RW, Choler P, Kikvidze Z, Michalet R, Pugnaire FI, Callaway RM (2004) Rethinking plant community theory. *Oikos* 107:433–438
- MacDougall AS, Gilbert B, Levine JM (2009) Plant invasions and the niche. *J Ecol* 97:609–615
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz F (2000) Biotic invasions: causes, epidemiology, global consequences and control issues. *Ecology* 5:1–20
- Mahner M, Bunge M (1997) Foundations of biophilosophy. Springer, Berlin
- Marone L, Galetto L (2011) El doble papel de las hipótesis en la investigación ecológica y su relación con el método hipotético-deductivo. *Ecología Austral* 21:201–216 (in Spanish)
- McCune B, Grace JB (2002) Analysis of ecological communities. MjM Software, Gleneden Beach, Oregon, USA. www.pcord.com. Accessed 29 April 2014
- McCune B, Mefford JB (2011) PC-ORD. Multivariate analysis of ecological data. Version 6.0
- Medina AA (2007) Reconstrucción de los regímenes de fuego en un bosque de *Prosopis caldenia*, provincia de La Pampa, Argentina. *Bosque* 28:234–240 (in Spanish)
- Medina AA, Dussart EG, Estelrich HD, Morici EA (2000) Reconstrucción de la historia del fuego en un bosque de *Prosopis caldenia* (Burk.) de Arizona, sur de la provincia de San Luis. *Multequina* 9:91–98 (in Spanish)
- Moles AT et al (2012) Invasions: the trail behind, the path ahead, and a test of a disturbing idea. *J Ecol* 100:116–127

- Ordoñez A, Olff H (2013) Do alien plant species profit more from high resource supply than natives? A trait-based analysis. *Glob Ecol Biogeogr* 22:648–658
- Ordoñez A, Wright IJ, Olff H (2010) Functional differences between native and alien species: a global-scale comparison. *Funct Ecol* 24:1353–1361
- Orians GH (1986) Site characteristics favoring invasions. In: Mooney HA, Drake JA (eds) *Ecology of biological invasions of North America and Hawaii*. Springer, New York, pp 133–145
- Parker JD, Burkepile DE, Hay ME (2006) Opposing effects of native and exotic herbivores on plant invasions. *Science* 311:1459–1461
- Patterson B, Pascual R (1972) The fossil mammal fauna of South America. In: Keast A, Erk F, Glass B (eds) *Evolution, mammals, and the southern continents*. State University of New York Press, New York, pp 247–309
- Pauchard A, Alaback PB (2004) Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of South-Central Chile. *Cons Biol* 13:238–248
- Pearson DE, Hierro JL, Chiuffo MC, Villarreal D (2014a) Rodent seed predation as a biotic filter influencing exotic plant abundance and distribution. *Biol Invasions* 16:1185–1196
- Pearson DE, Icasatti NS, Hierro JL, Bird BJ (2014b) Are local filters blind to provenance? Ant seed predation suppresses exotic plants more than natives. *PLoS ONE* 9(8):e103824
- Pickett STA, White PS (1985) *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando
- Pissolito C, Guerrero C (2016) *Taraxacum officinale* F. H. Wigg. In: Herrera I, Goncalves E, Pauchard A, Bustamante RO (eds) *Manual de plantas invasoras de Sudamérica*. Trama Impresores, Santiago, pp 24–25 **(in Spanish)**
- Prieto A (2000) Vegetational history of the Late glacial-Holocene transition in the grasslands of eastern Argentina. *Palaeo* 157:167–188
- Primer Inventario Nacional de Bosques Nativos, Segunda Etapa (2006) *Inventario de Campo en la Región Espinal*. Distritos Caldén y Ñandubay. Secretaría de Ambiente y Desarrollo Sustentable de la Nación, Buenos Aires, Argentina **(in Spanish)**
- Prina AO (1995) Las crucíferas de la provincia de La Pampa, República Argentina. *Revista de la Facultad de Agronomía* 8:29–67 **(in Spanish)**
- Richardson DM, Ricciardi A (2013) *Misleading criticisms of invasion science: a field guide*. Divers Distrib 19:1461–1467
- Rúgolo de Agrasar ZE, Steibel PE, Troiani HO (2005) *Manual ilustrado de las gramíneas de la provincia de La Pampa*. UNLPam-UNRC, Santa Rosa **(in Spanish)**
- Salomone F (2005) Desarrollo de un índice de abundancia relativa para ciervo colorado (*Cervus elaphus*) en la reserva provincial Parque Luro, La Pampa. Informe final. Consejo Federal de Inversiones Provincia de La Pampa **(in Spanish)**
- Seabloom EW, Borer ET, Martin BA, Orrock JL (2009) Effects of long-term consumer manipulations on invasion in oak savanna communities. *Ecology* 90:1356–1365
- Seabloom EW et al (2015) Plant species' origin predicts dominance and response to nutrient enrichment and herbivores in global grasslands. *Nat Commun* 6:7710
- Simberloff D, Vitule JR (2014) A call for an end to calls for the end of invasion biology. *Oikos* 123:408–413
- Simberloff D et al (2011) Non-natives: 141 scientists object. *Nature* 475:36
- Simberloff D, Martin J-L, Genovesi P et al (2013) Impacts of biological invasions: What's what and the way forward? *Trends Ecol Evol* 28:58–66
- Sousa WP (1984) The role of disturbance in natural communities. *Annu Rev Ecol Syst* 15:353–391
- Troiani H, Steibel P (2008) Reconocimiento de malezas: Región subhúmeda y semiárida pampeana. UNLPam, Colegio de Ingenieros Agrónomos de La Pampa, Santa Rosa
- Valéry L, Fritz H, Lefeuvre J-C (2013) Another call for the end of invasion biology. *Oikos* 122:1143–1146
- van Kleunen M, Weber E, Fischer M (2011) A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecol Lett* 13:235–245
- Veen GF, de Vries S, Bakker ES, van der Putten WH, Olff H (2014) Grazing-induced changes in plant–soil feedback alter plant biomass allocation. *Oikos* 123:800–806
- Walker LR, Willig MR (1999) An introduction to terrestrial disturbances. In: Walker LR (ed) *Ecosystems of disturbed ground*. Elsevier, Amsterdam, pp 1–16
- Yunque A (1957) *Historia de los argentinos*. Editorial Futuro, Buenos Aires **(in Spanish)**