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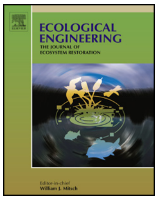

Identifying plant traits: A key aspect for species selection in restoration of eroded roadsides in semiarid environments

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ABSTRACT

Selecting suitable species for revegetation purposes represents a great challenge for practitioners and scientists, especially in semiarid regions where restoration projects often yield unsuccessful results. So far, little attention has been paid to plant traits related to species success in roadside ecosystems.

We aimed at (1) identifying plant traits associated with species success on four roadside situations that span a gradient of productivity and erosion stress and (2) providing an ecological base for selecting suitable species on the basis of their functional traits, applied to semiarid environments.

We tested the general hypothesis that trait distribution of successful roadslope colonizers results from a filtering process which is mainly controlled first by seed availability and dispersal and then by plant competition on north-facing roadfills and by environmental harshness on south-facing roadcuts. We analyzed the contribution of 10 plant traits selected as regards the prevailing limiting processes acting along the erosion-productivity gradient in semiarid roadslopes to species colonizing success.

A large database of 296 species × 10 traits based on leaf, seed and root measurements is provided.

Abundance in the neighbouring vegetation, ability of diaspores to long-dispersal and non-random trait filtering through abiotic and biotic filters, all influenced roadslope community assembly. Along the stress-productivity gradient, we observed strong shifts in the traits associated to species success. At the most productive end, species success was associated to a competitive-ruderal strategy (herbaceous successful species with high SLA and low LDMC values) and, at the harshest end, species success was related to seed resistance to removal by runoff and to resistance to drought (seed mucilage secretion and low index of seed susceptibility to removal).

We provide an ecological basis for selecting suitable species on the basis of morphological and functional plant traits, which is potentially of great benefit to practitioners and policy makers involved in roadside restoration in semiarid environments.

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1. Introduction

In the last decade both, restoration ecologists and practitioners agree that successful ecosystem restoration requires a sound scientific background based on an accurate understanding of ecological principles (Stokes et al., 2014; Temperton et al., 2004; van Andel and Aronson, 2006). Scientific knowledge of what are the constraints on membership in a community, of how species assemble, interact and function within a community, together with knowledge of the characteristics of the component species, is needed for the development of general guidelines for ecosystem restoration (Pywell et al., 2003; Temperton et al., 2004).

Assembly rules theory predicts that, out of a total species pool of potential colonizers (also called regional species pool), only those that are adapted to the abiotic and biotic conditions present at a site will be able to establish themselves successfully (sensu Keddy, 1992). However, before abiotic and biotic conditions can control the composition of the developing plant community, the actual arrival of viable diaspores by dispersion from the regional species pool determines the pool of applicant species waiting at the entrance of the community (Zobel, 1997). Thus, species membership in a community is constrained by successive environmental filters (dispersal, abiotic and biotic filters) that exclude all but a select subgroup of species from the total pool of potential colonizers. Because species interact with these filters through traits, the outcome of the filtering process will be reflected in the distribution of traits

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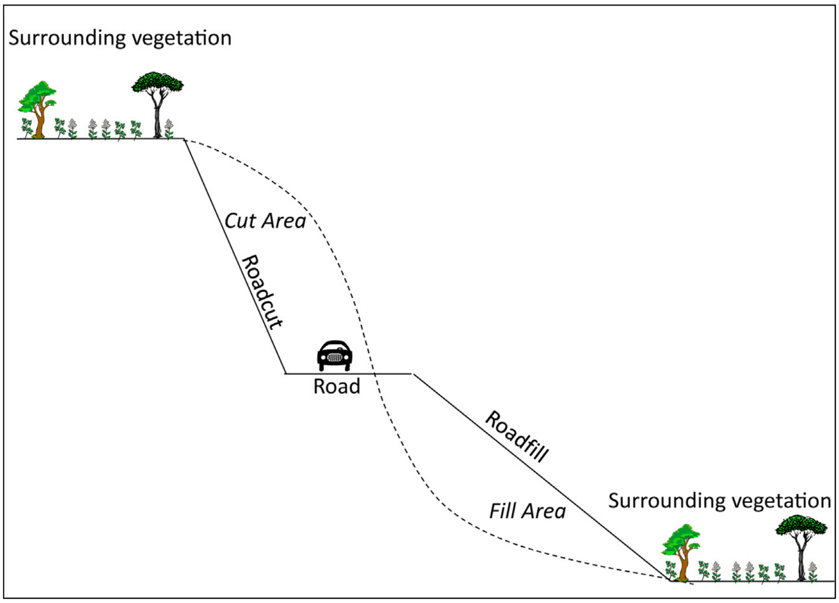

Fig. 1. Sketch of the two existing types of roadslopes, showing pre- (dotted line) and post-construction (solid line) contours. Roadcuts result from excavation and roadfills (=road embankments) from addition and compaction of unconsolidated materials. Surrounding vegetation areas to the roadslopes represent the pool of potential colonizers. Drawing not to scale.

Modified from Rentch et al. (2005).

among the co-occuring species in the community (Keddy, 1992). As a consequence, differences in trait distribution between the pool of potential colonizers and the developing community will provide useful information about the traits required to face the most limiting filters controlling species assembly in the community.

Roadsides are common worldwide ecosystems that have become a matter of serious concern for ecologists, conservationists, road engineers and the general public in the last decade (Schaffers and Sýkora, 2002; Steinfeld et al., 2007). This is due to the continuous extension of the worldwide road network as the world population increases and to the wide ecological impacts caused by road construction on the landscape (*i.e.* habitat fragmentation, soil erosion, invasion of exotic species, etc.) (Forman and Alexander, 1998; Steinfeld et al., 2007). Notwithstanding, the ecological functioning of roadside plant communities has been scarcely studied yet (Schaffers and Sýkora, 2002; Valladares et al., 2008). Roadside plant communities represent a unique opportunity to test assembly rules and study plant trait filtering using applied ecology (de la Riva et al., 2011). They also represent a great challenge for ecological restoration and for the selection of suitable species for roadslope revegetation, especially in arid and semiarid regions where many restoration projects yield unsuccessful results (Bochet and García-Fayos, 2004).

Recent studies on spontaneous colonization of semiarid roadslopes reveal that plant establishment in the early stages follows a process of primary succession whereby floristic composition is mainly shaped by the arrival of diaspores from the closest neighbourhood (Bochet et al., 2007a; Mola et al., 2011). Once diaspores have reached the exposed slopes, abiotic conditions represent the first limiting filter to plant recruitment (Tormo et al., 2006; Valladares et al., 2008). However, the strength of abiotic constraints in semiarid conditions depends on the type and aspect of roadslopes, decreasing from roadcuts to roadfills and from south to north-facing roadslopes (Bochet et al., 2010a; see Fig. 1 for roadslope type definition), and following a general trend of increasing soil fertility and water availability for plants and a decreasing erosion severity and soil compaction (Bochet and García-Fayos, 2004; Bochet et al., 2007b). As a result, vegetation cover increases along this “erosion-productivity” gradient giving rise to large differences in plant cover between the south-facing roadcuts and north-facing roadfills (*i.e.* 5% and 78% mean cover, respectively, in Bochet and García-Fayos, 2004) and to an increasing strength of the biotic filter (*i.e.* plant competition). Specific composition of plant communities along this gradient shows clear differences between the four roadslope categories (Bochet and García-Fayos, 2004) suggesting that plants from a specific roadslope category community may share the same attributes that make these plants able to cope with the specific abiotic and biotic conditions of their respective communities.

So far, very little attention has been paid to the identification of plant traits of successful colonizers in roadside communities (but Será, 2010; Karim and Mallik, 2008 for roadfills; de la Riva et al., 2011 for roadfills and roadcuts but without considering slope aspect).

In this study, we aim at (1) identifying plant traits associated with species success on four roadside situations that span a gradient of productivity and erosion stress and (2) providing an ecological base for selecting suitable species on the basis of their functional traits, applied to semiarid environments, which is potentially of great benefit to practitioners and policy makers involved in roadslope restoration.

We test the general hypothesis that trait distribution of successful roadslope colonizers results from a filtering process which is mainly controlled first by seed availability and dispersal and then by plant competition on north-facing roadfills and by environmental harshness on south-facing roadcuts. We expect that ruderal species with a high colonizing ability will be successful on all roadslope categories (annuals and herbaceous with a short life-cycle, long-dispersed and abundant in the surrounding vegetation), that successful colonizers on roadfills (mainly north-facing) will preferentially display a high ability to grow fast and compete (competition-related traits), and that successful colonizers on roadcuts will display a high ability to resist seed or plant removal by runoff and to cope with water-stressed conditions (erosion- and drought-related traits).

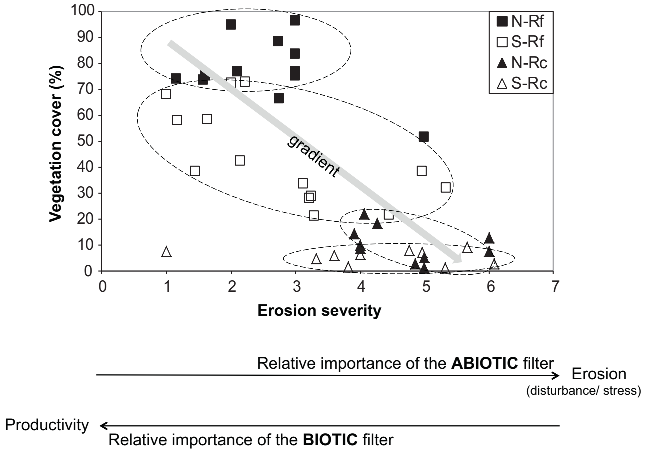

Fig. 2. Relationship between erosion severity and vegetation cover for the four different roadslope categories, highlighting the existence of a productivity-erosion gradient from north-facing roadfills to south-facing roadcuts (N-Rf: north-facing roadfill; S-Rf: south-facing roadfill; N-Rc: north-facing roadcut; S-Rc: south-facing roadcut). It is assumed that the relative importance of the environmental filters controlling plant assembly, and the resulting trait filtering process, changes along the gradient. We expect that biotic conditions are more limiting in roadfills and abiotic ones more constraining in roadcuts. The erosion severity index which varies from 0 to 9 was estimated on the basis of rill, gully and mass movement density on roadslopes. Data from Bochet and García-Fayos (2004).

2. Materials and methods

2.1. Site description

This study was carried out in the Region of "La Plana Utiel-Requena" from the Valencian Community, East Spain (39°29′ N; 1°06′ W). The climate is semiarid with an annual mean temperature of 14.2 °C and an average annual precipitation of 418 mm (Pérez, 1994). Annual precipitation is concentrated in May and October. Frost events occurring in winter and droughts associated with the summer period constrain vegetation development. Soils are derived from calcareous marls and clays from Tertiary origin.

We selected 36 eight year old roadslopes with angles ranging from 25° to 45° between km 267 and 307 of the A3-highway (Madrid-Valencia) and divided them in four categories: seven north-facing roadfills (NRf), nine south-facing roadfills (SRf), nine north-facing roadcuts (NRc) and eleven south-facing roadcuts (SRc). Bochet and García-Fayos (2004) provided evidence of an increasing gradient of environmental harshness according to these roadslope categories and the existence of a resulting productivity-erosion gradient in the following direction: NRf, SRf, NRc, SRc (Fig. 2).

The area surrounding the roadslopes was primarily agricultural (vineyards), but included also remains of Mediterranean shrublands. It was similar between roadfills and roadcuts and between north and facing slopes considered.

2.2. Vegetation surveys

From March to June 2000, species were identified and recorded in all roadslopes and in their corresponding surrounding area to a distance of 150 m from the slope border. The sampling area was proportional to the size of the roadslopes and ranged from 70 to 7900 m^2. Although the size of the sampling area was different in all cases, its distribution was homogeneous between the four categories of roadslopes considered in the analyses ($F_{3,32} = 0.567$; $P = 0.641$).

Species colonizing success on roadslopes was assessed for the four roadslope categories. Since we aimed at identifying traits of species with a potential role in soil protection against erosion on roadslopes, we used a criteria of success based on the combination of species frequency and abundance on roadslopes. With these criteria, we aimed at identifying the ability of a given species to reach the slope, to germinate, to grow, to reproduce itself and to maintain its populations in a so large number of slopes and with a so high abundance that it can be considered helpful for restoration purposes.

Species frequency was defined as the percentage of roadslopes where the species occurred. Relative abundance of each species was estimated in all roadslopes and surrounding areas according to four classes, following the procedure described in detail in Bochet et al. (2010b): class 0 = no individuals, class 1 = less than 10 individuals scattered along the surveyed area, class 2 = individuals present either regularly or in local monospecific patches, and class 3 = individuals abundantly present and dominant along the surveyed area. Species were classified as "successful colonizers" (SUC_COL) when they were present in more than 50% of the roadslopes surveyed per category and when their relative abundances were equal or greater than class "2" in at least one-third of the roadslopes where they occurred. If both requirements were not fulfilled, the colonizing species was considered "unsuccessful". We also defined a "NO_COL" pool of species corresponding to those species living in the surrounding areas of a specific roadslope category but unable to colonize the corresponding roadslope category and absent from this latter.

The very low number of hydroseeded species that survived eight years after being sown (Bochet and García-Fayos, 2004) was not included in the species lists as our main interest relied on the colonizing ability of native species from the regional species pool. Moreover, the available data about hydroseeded roadslopes and hydroseeded species used during hydroseeding provided by the public administration were not reliable as the hydroseeded species listed did not always match with the ones recorded in the vegetation surveys.

Species nomenclature followed the Iberian Flora (Castroviejo, 1986–2012) and, for the still unpublished species in the Iberian Flora, we followed the Flora of Valencia (Mateo Sanz and Crespo Villalba, 1998).

2.3. Trait measurements

All species recorded were described in terms of 10 key traits listed and defined in Table 1. Trait selection accounted for ecologically relevant traits that we presume are involved in roadslope colonization (including seed dispersal-, competition-, erosion- and drought-related traits; see Table 1). Selected traits, except those specifically related to erosion and drought resistance (mucilage secretion, seed susceptibility to removal by runoff, plant sprouting ability and root morphology), match those from the minimal LEDA list of functional plant traits (Kleyer et al., 2008) and follow the nomenclature and measurement procedures of Cornelissen et al. (2003). A full description of the traits can be found in Cornelissen et al. (2003).

Trait information was obtained from field and laboratory observations and measurements, except for longevity and woodiness data that were compiled from floras (Table 1). Leaf trait measurements were conducted on 10 leaves/species, each leaf corresponding to a different individual. We measured the specific leaf area (SLA, one-sided area of a fresh leaf divided by its oven-dry mass) and leaf dry matter content (LDMC, oven-dry mass of a leaf divided by its water saturated fresh mass).

Seed measurements were performed on 25 air-dried seeds from a larger pool of seeds collected from at least 10 different individuals per species. In case of indehiscent fruits, seeds were extracted by removing the covering fruit structures before seed measurements

Table 1
Description of plant traits and abbreviations used in the tables, compilation sources and ecological relevance for plant colonization on roadslopes.

Trait category	Trait	Abbreviation	Scale and Unit	Information compilation source	Ecological relevance
General plant traits					
	Longevity	LIFE	Categorical annual *vs.* perennial	Field observation and literature[a]	Longevity, ruderality
	Woodiness	WOOD	Categorical herbaceous *vs.* woody	Field observation and literature[a]	Longevity, ruderality
Seed-related traits					
	Dispersal strategy	DIST	Categorical long-distance *vs.* short-distance	Field observations, inference from morphology and literature[b]	Dispersal
	Mucilage	MUC	Categorical mucilage (myxospermy) *vs.* no-mucilage	Field harvesting and laboratory measurements	Response to disturbance Response to stress
	Seed mass	SEMA	Continuous (g)	Field harvesting and laboratory measurements	Seedling growth
	Seed susceptibility to removal	SSR	Continuous (dimensionless, varies from 0 to 1)	Field harvesting and laboratory measurements, and calculations	Response to disturbance
Root-related traits					
	Root type	ROOT	Categorical tap-root *vs.* branched	Field excavations and observations, and literature[c]	Response to disturbance
	Sprouting	SPRO	Categorical sprouter *vs.* non-sprouter	Field excavations and observations, and literature[c]	Response to disturbance
Leaf-related traits					
	Specific Leaf Area	SLA	Continuous ($mm^2\ mg^{-1}$)	Field harvesting and laboratory measurements	Seedling growth, Competitive ability
	Leaf Dry Matter Content	LDMC	Continuous ($mg\ g^{-1}$)	Field harvesting and laboratory measurements	Nutrient adquisition and retention of captured resources

[a] Mateo Sanz and Crespo Villalba (1998).
[b] Molinier and Müller (1938), van der Pijl (1972) and Hensen (1999).
[c] Guerrero-Campo (1998); Kleyer et al. (2008, LEDA Traitbase).

were performed. Air-dried seeds were weighed to 10 μg precision. Plant capacity to develop seeds with a mucilaginous coat (myxospermy), an advantage to resist seed removal by runoff on steep slopes and to increase germination success in water-stressed environments (García-Fayos et al., 2013; Gutterman and Shem-Tov, 1996; Harper and Benton, 1966), was measured following the procedure of Engelbrecht et al. (2014). Seed susceptibility to removal by runoff (SSR index) was calculated following the procedure of García-Fayos et al. (2010). SSR values range from zero to one, corresponding to 0 and 100% seed removal, respectively.

Species were assigned to two broad dispersal categories: “long-distance dispersal” including anemochores, endo- and exozoochores, and “short-distance dispersal” referred to barochores, autochores, ballistics and myrmecochores (more details in Bochet et al., 2009). They were also assigned to two longevity (annual *vs.* perennial) and two woodiness (herbaceous *vs.* woody) categories according to field observations and literature data (Mateo Sanz and Crespo Villalba, 1998).

Sprouting capacity was defined as the ability of plants to form new shoots from the basal or below plant parts after removal of the above-ground biomass. Assessment of sprouting capacity was based on field observations and excavations of three to five different individuals per species. The same excavations enabled the description of root morphology according to two classes: tap- *vs.* branched-roots. The tap-rooted class includes species with one main, straight, thick, tap root and several fine lateral roots, whereas the branched class includes species with a non-dominant primary root which branches into many thinner secondary roots which, in turn, rebranch into numerous finer tertiary roots. The sprouting capacity and root morphology are both related to plant persistence in eroded and water-stressed areas (de Baets et al., 2009; Guerrero-Campo, 1998).

For continuous traits we used the mean value of all replicates per species.

2.4. Statistical analyses

The influence of species abundance in the surrounding areas on species colonizing success on roadslopes was analyzed by means of logistic regressions. The resulting Wald statistic and Nagelkerke’s R^2 values describe the significance and strength, respectively, of the relationship between both variables.

To assess the significance of the contribution of dispersal strategy, degree of woodiness, seed ability to produce mucilage, seed mass, seed susceptibility to removal, root sprouting capacity, root type, specific leaf area and leaf dry matter content in determining species colonizing success we fitted Generalized Linear Models and performed Deviance analysis to determine the contribution of traits to the variation of species colonizing success. We assumed a binomial distribution of errors with a “logit” link for the response variable, species colonization success (1 = success, referring to successful species or SUC-COL species pool *vs.* 0 = failure, referring to species unable to colonize the slopes or “NO-COL” species pool). Models were fitted separately for each roadslope category. Previously, we used Variance Inflation Factors to assess which explanatory variables were collinear and should be dropped from the model before the analyses (Zuur et al., 2009).

Abundance analyses were performed with SPSS v.19.0 statistical Package (SPSS Inc., Chicago, IL, USA) and R v.2.15.2 software was used to fit General Linear Models, perform Deviance analyses

Table 2
Frequencies of species (%) according to the categorical traits studied, in the two species pools (SUC_COL: successful colonizers on roadslopes and NO_COL: potential colonizers in the surrounding area unable to colonize the roadslopes) and in the four roadslope categories (NRf: north-facing roadfill, SRf: south-facing roadfill, NRc: north-facing roadcut, SRc: south-facing roadcut). As all traits are bicategorical, frequencies are only given for one trait category indicated between brackets. Trait abbreviations are described in Table 1.

Trait		NRf	SRf	NRc	SRc
DIST (long-distance)	SUC_COL	71.4	70.4	75.0	55.6
	NO_COL	34.5	28.9	32.5	33.6
LIFE (annual)	SUC_COL	67.9	51.9	60.0	38.9
	NO_COL	39.1	31.6	35.7	36.6
WOOD (herbaceous)	SUC_COL	100	96.3	100	83.3
	NO_COL	72.7	60.5	68.2	71.6
SPRO (sprouter)	SUC_COL	7.1	11.1	10.0	22.2
	NO_COL	33.3	36.0	30.3	32.3
ROOT (tap-root)	SUC_COL	53.6	59.2	50.0	55.6
	NO_COL	50.9	40.4	48.0	47.2
MUC (secretion)	SUC_COL	10.7	18.5	15.0	27.8
	NO_COL	11.4	13.5	11.2	10.1

and Variance Inflation Factors, with *glm* and *anova* functions from "stats" package, and *vif* function from "car" package, respectively (available from http://www.R-project.org).

3. Results

In total, 296 species were identified in the surrounding area of the roadslopes as potential roadslope colonizers (see Appendix A with detailed information of trait data for the 296 species). More specifically, 214, 243, 251 and 242 species were recorded in the respective surrounding area of NRf, SRf, NRc and SRc roadslopes. From these species pools, 51%, 47%, 63% and 55% species were unable to colonize the NRf, SRf, NRc and SRc roadslopes, respectively (NO_COL species) and 13%, 11%, 8% and 7% species were classified as successful colonizers (SUC_COL) in the respective roadslope categories.

Species abundance in the neighbouring vegetation was a significant predictor of species colonizing success in all roadslope categories ($\text{Wald}_{\text{NRf}} = 30.549$, $P < 0.001$; $\text{Wald}_{\text{SRf}} = 37.351$, $P < 0.001$; $\text{Wald}_{\text{NRc}} = 31.014$, $P < 0.001$; $\text{Wald}_{\text{SRc}} = 26.950$, $P < 0.001$). The strength of the relationship between both variables was 51%, 49%, 49% and 48% in NRf, SRf, NRc and SRc roadslopes, respectively (Nagelkerke's R^2 values).

Because collinearity analysis showed VIF values higher than 2 for the longevity trait (LIFE), we fitted generalized linear models for species success using all the studied traits, but longevity. The amounts of deviance accounted for the general linear models were 27%, 34%, 26% and 17% for NRf, SRf, NRc and SRc roadslopes, respectively. Dispersal strategy influenced significantly species success in all roadslope categories (Pr(>Chi) < 0.04 in all models) and was the most contributing trait to species success in NRf, SRf and NRc roadslopes (8%, 11% and 9% of the deviance, respectively), indicating that colonizing success was related first to the ability of species to long-distance dispersal (Table 2). Long-dispersal affected positively species colonizing success (Table 2). SLA influenced significantly and positively species success in all roadslope categories, but SRc (Pr(>Chi) = 0.0370, 0.0012, 0.0423 for NRf, SRf, NRc, respectively, see Table 3). LDMC also affected significantly, but negatively, species success on roadfills (Pr(>Chi) = 0.0049 and 0.0017 for NRf and SRf, respectively, Table 3). The degree of woodiness affected significantly species success on NRf and NRc roadslopes, with a significant contribution of herbaceous species to species success (Pr(>Chi) = 0.02595 and 0.0115, respectively, Table 2). Seed ability to produce mucilage influenced significantly (or marginally significantly) and positively species success in all roadslope categories, but NRf (Pr(>Chi) = 0.040, 0.060 and 0.014 in SRf, NRc and SRc, Table 2), and in SRc roadslopes, mucilage was the most important trait contributing to species success (6% of the deviance). Seed susceptibility to removal decreased along the productivity-erosion gradient, with a general decreasing trend in SSR mean value in the SUC_COL pool from 0.13 in NRf to 0.06 in SRc roadslopes, indicating a higher resistance of seeds to removal by runoff along this gradient (Table 3). However, the influence of this trait on species success was significant only for SRf and NRc, even though the SSR mean values were the same in the SUC_COL and NO_COL species pools in NRc and SRc slopes (SSR = 0.06 and 0.11, respectively for the two pools, Table 3). The other traits that were analyzed had no significant effect on species success.

Table 4 provides an overview of trait significance in species success in the four roadslope categories and highlights general shifts in trait distribution of SUC_COL plant communities along the productivity-erosion gradient.

4. Discussion

Our study highlights the importance of plant traits required to successfully face the most limiting environmental filters in the colonization process of roadslopes along an erosion-productivity gradient. First, it underlines the influence of species abundance in the neighbouring vegetation, together with an efficient dispersal mechanism (long-distance dispersal), in species colonizing success in all roadslope categories along the gradient. Our results also give insight into the mechanisms that control early assembly of roadslope plant communities along an erosion-productivity gradient in semiarid regions, once the seeds have reached the roadslopes.

Table 3
Mean values ± standard errors of continuous traits in the four roadslope categories (NRf: north-facing roadfill, SRf: south-facing roadfill, NRc: north-facing roadcut, SRc: south-facing roadcut) and in the two species pools (SUC_COL: successful colonizers on roadslopes and NO_COL: potential colonizers in the surrounding area unable to colonize the roadslopes). Trait abbreviations are described in Table 1.

Roadfills	NRf		SRf	
	SUC_COL (mean ± S.E.)	NO_COL (mean ± S.E.)	SUC_COL (mean ± S.E.)	NO_COL (mean ± S.E.)
SLA ($\text{mm}^2\ \text{mg}^{-1}$)	17.65 ± 1.11	14.65 ± 0.64	18.03 ± 1.02	13.38 ± 0.59
LDMC (mg g^{-1})	207.68 ± 13.05	281.12 ± 12.49	216.13 ± 12.13	285.86 ± 11.68
SEMA (g)	0.00357 ± 0.00111	0.00529 ± 0.00111	0.00414 ± 0.00124	0.00442 ± 0.00078
SSR	0.13 ± 0.03	0.13 ± 0.02	0.09 ± 0.03	0.11 ± 0.01
Roadcuts	NRc		SRc	
	SUC_COL (mean ± S.E.)	NO_COL (mean ± S.E.)	SUC_COL (mean ± S.E.)	NO_COL (mean ± S.E.)
SLA ($\text{mm}^2\ \text{mg}^{-1}$)	17.43 ± 1.20	14.87 ± 0.54	15.98 ± 1.44	15.25 ± 0.59
LDMC (mg g^{-1})	244.21 ± 22.41	170.16 ± 10.38	237.72 ± 23.44	268.31 ± 11.28
SEMA (g)	0.00477 ± 0.00139	0.00503 ± 0.00084	0.00408 ± 0.00133	0.00582 ± 0.00106
SSR	0.06 ± 0.02	0.11 ± 0.01	0.06 ± 0.02	0.11 ± 0.01

Table 4
Summary table showing the gradual change in plant trait distribution in the pool of successful colonizers (SUC_COL) across the four roadslope categories (NRf: north-facing roadfill; SRf: south-facing roadfill; NRc: north-facing roadcut; SRc: south-facing roadcut) and along the productivity-erosion gradient (from NRf to SRc). Grey cells indicate traits that contribute significantly to species success and "0-white" cells indicate traits that do not contribute significantly to species success. "+" and "-" symbols indicate the sign of the contribution (in the case of categorical traits, with respect to the trait category indicated between brackets). "(+)" symbol indicates a marginal significance of the trait contribution. Due to its collinearity with other traits, LIFE was neither included in the glm nor in this table. Trait abbreviations are described in Table 1.

Trait	NRf	SRf	NRc	SRc
DIST (long-distance)	+	+	+	+
SLA	+	+	+	0
LDMC	–	–	0	0
WOOD (herbaceous)	+	0	+	0
SEMA	0	0	0	0
SPRO (sprouter)	0	0	0	0
ROOT (tap-root)	0	0	0	0
SSR	0	–	–	0
MUC (secretion)	0	+	(+)	+

As expected, along the erosion-productivity gradient, colonizing success was found to be dependent upon the presence of suitable traits adapted to the specific limiting processes prevailing in each roadslope category. At the most productive end of the gradient, in NRf slopes, successful species were mainly herbaceous and they displayed relatively high SLA and low LDMC values. Because in our set of species herbaceous species are highly associated to short longevity ($\chi^2 = 72.06$, $p < 0.0001$), we suggest that not only the habit of being herbaceous but also having a short-life cycle positively contribute to species success on these slopes. SLA has often been used as a surrogate of relative growth rate and plant competitive ability, and LDMC has often been used as an indicator of efficiency of nutrient conservation and slow rates of carbon gain (Cornelissen et al., 2003; Garnier et al., 2004). Thus, species success on NRf roadfills showed to be related to a competitive-ruderal life strategy (RC, sensu Grime, 1979) of plants exhibiting a short-life cycle, high colonizing capacity, high growing rates and a high competitive ability. Conversely, failure in this slope category was associated to long-life cycles and slow-growing and nutrient conservative species.

According to our hypothesis, a different set of traits was associated to establishment success in the opposite end of the gradient, in SRc roadcuts. Here, successful species were mainly characterized by mucilage-secreting seeds and low SSR values, lower than that recorded on NRf roadfills. Both traits provide seeds with a high resistance to removal by runoff on steep slopes. Previous studies showed that seeds that secrete mucilage in contact with water exhibit lower removal rates from steep slopes than non-secreting mucilage seeds of similar weight (García-Fayos and Cerdà, 1997; García-Fayos et al., 2010). Moreover, in semiarid badlands, where erosion and water-stress are high, mucilage secretion has proved to be an advantage for species living on steep slopes (Bochet et al., 2009; García-Fayos et al., 2013). Mucilage avoids seed removal downhill, where seeds can get buried deep into the soil or suffer severe competition with other more competitive plants and plays a role in seed germination by increasing both, the water retention capacity of seeds and the seed–soil particle contact (Engelbrecht et al., 2014; Gutterman and Shem-Tov, 1996, 1997; Huang et al., 2008; Lu et al., 2010). The critical duration of water availability in the soil for seed germination in SRc roadcuts (Bochet et al., 2007b) may also explain why myxospermy was the most contributing trait to species success in this roadslope category.

In the intermediate roadslope categories within the gradient (SRf and NRc), successful species shared some traits with NRf- and some others with SRc-successful species, indicating that the changes in trait distribution along the gradient are gradual. Displaying high SLA values was an advantage to be successful in SRf and NRc as in NRf roadslopes and displaying seeds able to produce mucilage and with low SSR values was an advantage to be successful on SRf and NRc as in SRc roadslopes. However, low LDMC values were significantly related to success in SRf (as in NRf), but not in NRc roadslopes where there is a higher environmental pressure.

Overall, the productivity-erosion gradient strongly influenced traits of successful colonizers with a differential selection of colonizing- and competition-related traits in NRf and of erosion-related traits in SRc roadslopes. In the intermediate roadslope categories, SRf and NRc, where both processes simultaneously act on species filtering, a combined selection of traits related to both, competition and erosion, occurred.

To our knowledge, this is the first time that the influence of a gradual change in the filtering process on plant traits is described along an erosion-productivity gradient in roadslopes, emphasizing the duality of environmental filters at both ends of the gradient. However, our study also emphasizes the importance of a previous filter based on seed availability and dispersal capacity from the surrounding areas to the roadslopes, that act before the seeds reach the roadslopes.

Previous studies have related the occurrence of annual, herbaceous species with wind-dispersed seeds and a low allocation to below-ground parts to road habitats, mainly roadfills, in a wide range of climatic conditions (Karim and Mallik, 2008; Será, 2010). However, thus far, roadcut plant communities have received no attention as regards trait characterization. In the only attempt, to our knowledge, that aimed at identifying plant traits in both, roadfill and roadcut plant communities (but without considering slope aspect), de la Riva et al. (2011) failed to find different specific traits associated to both types of roadslope plant communities under a wetter climate. After examining a set of easy-achievable traits from the literature, these authors reported that dominant species on both types of roadslopes shared common syndromes (wind-pollinated, large-seeded and non-native).

The *a priori* selection of traits, specifically related to the prevailing filtering mechanism that act in the different roadslope categories, may explain the successful identification of different traits along the erosion-productivity gradient in our study area. Although more time-consuming and laborious to measure than most of the easily-achievable traits found in the flora and literature, the *ad-hoc* selection of erosion- and competition-related traits has been a key issue in the discrimination of successful traits between the four roadslope categories. Whereas SLA and LDMC are well-known traits that have been used in many studies on plant traits associated to other types of disturbances (grazing, fire, mowing, etc.), erosion-related traits such as myxospermy and SSR have received very little attention to date in the literature. As regards myxospermy, our results are consistent with the few studies that describe this plant trait in natural plant communities of highly eroded badlands in a semiarid area of East Spain. In a similar approach to the present study, Bochet et al. (2009) found higher frequencies of myxospermic species in the pool of colonizers on south- and west-facing badland slopes than in the pool of potential colonizers from the regional pool that were unable to colonize these slopes. Moreover, in the same badland area, García-Fayos et al. (2013) found that the proportion of myxospermic species varied among plant communities that differed in the severity of soil erosion and that this proportion correlated with soil properties linked to runoff generation. These coincident results support the idea that mucilage secretion, a seldom studied trait, plays a crucial role in the fixation of seeds to natural or artificial steep slopes against runoff pressure (see Bochet, 2015 for a review).

Nevertheless, other traits -as sprouting and tap-roots-that proved to favour plants living on badlands where severe erosion causes a simultaneous increase in stress and disturbance (Guàrdia, 1995; Guerrero-Campo et al., 2008), did not show any significant relation with species colonizing success on the harshest SRc roadslope conditions. We also failed to find a positive relationship between seed mass and species colonizing success that we expected in the most productive roadslope categories, as seeds with more food reserves proved to generate more competitive seedlings with higher establishment success in different productive habitats (Moles and Westoby, 2004).

Our results also give insight into the mechanisms that control early assembly of roadslope plant communities along an erosion-productivity gradient in semiarid regions. According to the dispersal-based neutral hypothesis of plant assembly, species are randomly selected as regards traits and the probability of colonizing a site merely relies on the availability of diaspores in the nearby vegetation and on their capacity to long-disperse and reach the site (Hubbell, 2001). This hypothesis is fulfilled if any other trait – besides dispersal capacity – does not matter at all in roadslope community assembly. Here, even though species abundance in the neighbouring vegetation and species capacity to long-disperse positively influenced species colonizing success, the distribution of trait values along the erosion-productivity gradient within the roadslope communities of successful species was clearly non-random. Differences in the distribution of several traits, not related to dispersal, between the compared pools of species in all roadslope categories indicated that species traits were a major component of species success or failure. Therefore, abundance in the nearby vegetation, dispersal and trait filtering through environmental sieves once the diaspores have reached the slopes, all take part in roadslope community assembly. Similar results were described by Kirmer et al. (2008) in another man-made ecosystem. These authors reported that the probability of colonizing mined sites was mainly determined by species abundance in the regional species pool, dispersal traits, and also other trait-based processes.

Our study has also clear applications for roadslope restoration in semiarid regions, where active restoration is needed to reach an extensive vegetation cover and mainly relies on the improvement of abiotic conditions and the introduction of appropriately selected species (Bochet et al., 2010a). However, the introduction of species in the course of restoration still remains a critical challenge that requires the provision of sound scientific knowledge and practical guidelines (Haan et al., 2012; Hölzel et al., 2012). Our study provides an assembly-based approach for selecting suitable native plants on the basis of their traits that helps to fill this gap and has an important advantage as regards approaches based on species names already proposed for roadslopes in a large range of climatic conditions (*i.e.* Bochet et al., 2010b; Cilliers and Bredenkamp, 2000; Godefroid and Tanghe, 2001; Heindl and Ullmann, 1991; Ullmann et al., 1995). While lists of species names are site-specific and not easily comparable among sites, trait-based characterizations can be easily transferred and applied across restoration projects at a broader scale, whatever the regional settings and local species pools (Fischer et al., 2013; Pywell et al., 2003). Thus, our study provides insight into the traits related to plant colonizing success on roadslopes and highlights for the first time important differences in trait characterization of successful species among the different roadslope categories with respect to slope type and aspect.

As a consequence, the widespread and common use of a same seed mixture for all roadslope categories at a site, whatever the roadslope type and aspect, looks inappropriate for roadslope revegetation. Alternatively, species composition of seed mixtures should be selected according to the plant traits required to face the respective environmental filters prevailing in the different roadslope categories.

Therefore, when species introduction is to proceed, we recommend the use of fast-growing and highly competitive species (annual, herbaceous, high SLA and low LDMC values) on north-facing roadfills and of species able to resist seed removal by runoff and water stress in south-facing roadcuts (myxospermic seeds, low SSR values). On these latter slopes, additional traits related to plant ability to control erosion could also be considered in order to improve slope stabilization after vegetation establishment (de Baets et al., 2009; Stokes et al., 2014). On south-facing roadfills and north-facing roadcuts, the use of annual, herbaceous species with seeds able to resist removal by runoff is recommended. However, on south-facing roadfills species should moreover display a high ability to compete (high SLA values).

However, this research and numerous other ones in the bibliography also highlight the great capacity for natural colonization of roadslopes through the surrounding areas (*e.g.* Bochet et al., 2007a; Mola et al., 2011). This is why the use of active restoration (*e.g.* species introduction), which tends to be costly and to involve great uncertainty, should be recommended only in extreme situations (Bochet et al., 2010a; Matesanz et al., 2006).

We encourage the inclusion of the novel traits related to erosion resistance (myxospermy and SSR index), proposed in the present study, in the general lists of traits available in the literature that describe relevant functional and morphological traits related to different types of disturbances (*i.e.* Cornelissen et al., 2003; Kleyer et al., 2008). We also encourage the use of these traits in future studies on traits in plant communities of severely eroded environments.

In conclusion, these new insights from basic ecology and practical management guidance represent a great opportunity for practitioners to move forward with the success of roadslope restoration in semiarid environments, which currently leaves a lot to be desired.

5. Conclusions

Our study highlights for the first time important differences in plant traits along an erosion-productivity gradient of roadslopes that support a differential trait-based selection of species as regards roadslope type and aspect. Erosion- and drought-resistant traits, in the case of roadcuts, and ruderality/competition-related traits, in the case of roadfills, should be taken into account to improve the efficiency of revegetation programmes in semiarid conditions.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecoleng.2015.06.019

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