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Plant species colonization in newly created road habitats of South Korea: Insights for more effective restoration

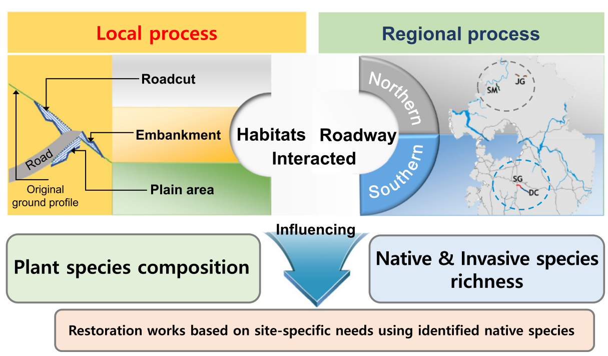
Deokjoo Son [a], Josu G. Alday [b,c], Yeounsu Chu [d], Eun Ju Lee [a], Shinyeong Park [a], Hyohyemi Lee [d,*]

[a] School of Biological Sciences, Seoul National University, Seoul 08826, South Korea
[b] Joint Research Unit CTFC - AGROTECNIO, Av. Alcalde Rovira Roure 191, E25198 Lleida, Spain
[c] Dep. Crop and Forest Sciences, University of Lleida, Av. Alcalde Rovira Roure 191, E25198 Lleida, Spain
[d] National Institute of Ecology, Seocheon 33657, South Korea

HIGHLIGHTS

- Ecological restoration is limited by illiteracy of naturally formed plant communities in degraded sites.
- Four S Korean roadway plant communities were monitored to have insights on restoration potential.
- Habitats such as embankments, plain areas, and roadcuts conditioned plant species composition.
- Regional and local process interacts making complex plant colonization or compositional patterns.
- Restoration plans should base on plant species established spontaneously in road degraded areas.

GRAPHICAL ABSTRACT



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ABSTRACT

Despite the advances in restoration methods for newly created road habitats such as roadcuts and embankments, implementation in different parts of the world is limited by high cost and lack of knowledge of naturally formed plant communities. However, a cheaper alternative is to relay in natural successional process in sites under optimal conditions. Thus, the first steps should focus on identifying plant species that colonize roadways and road habitats as well as optimal colonization sites. Our study aimed to describe species composition, exotic species presence, and diversity among four roadways (Jeongok-Youngjung, JG; Seolma-Gueup, SM; Singal, SG; and Samga-Daechon, DC) and three habitat types (embankments, plain areas, and roadcuts) in South Korean peninsula. The effect of some environmental factors on plant composition was also examined (soil type, soil slope, and surrounding landscape). Our results showed that established plant species composition was influenced by the interaction between roadways and habitats types, which was also the main interaction affecting plant richness and evenness. Surprisingly, environmental variables had no effect on plant species composition, with a residual amount of explained variation. A total of 48 plant species were described as indicator of different roadways and habitat types, and 50% of them were invasive or cultivated species. It appeared that different regional-dependent processes, such as northern vs. southern roadways, interact with local process in new-road habitats, producing complex patterns of plant species colonization and composition. Thus, ecological restoration solutions should be targeted at site-specific needs (local) while taking into consideration the differences between northern and southern roadways (regional). Here, regional-pool and local-constraints interaction controls plant

* Corresponding author.
E-mail address: hyohyemi@nie.re.kr (H. Lee).

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composition and diversity during road construction in South Korea. Finally, new restoration actions should be based on plant species that have been established spontaneously in these degraded areas.

1. Introduction

Linear infrastructures such as motorways, railways, and pipelines are important elements for society development (van der Ree et al., 2011). However, linear infrastructures produce significant effects on adjacent habitats (Neher et al., 2013), and ecosystems, generating severe environmental degradation, fragmented landscapes, and finally biodiversity loss (Bochet and García-Fayos, 2004; van der Ree et al., 2011). Road construction is a major linear disturbance that disrupts the connectivity of ecosystems and creates new habitats such as roadcuts and embankments. During road construction, works such as vegetation clearing, addition of road-fill, and grading of unpaved roads generate new exposed areas that are prone to colonization by exotic species, creating novel plant communities (Gelbard and Belnap, 2003; Trombulak and Frissell, 2000). In addition, roads are considered to be a major corridor for the ongoing spread of exotic plants (Gelbard and Belnap, 2003) due to factors such as the transport of propagules by cars (Sharma and Raghubanshi, 2009).

One of the major effects of road construction is the formation of roadcuts and embankments, which are characterized by bare, steep slopes that are eroded by the direct action of rainfall and soil surface runoff (Bochet and García-Fayos, 2004). Roadcuts and embankments are also characterized by low contents of soil nutrients and high soil compaction (Jimenez et al., 2013). These newly created habitats are usually revegetated (e.g., hydroseeding) right after their constructions (Alday et al., 2010), or left to undergo natural re-colonization by spontaneously established plants (Bouchet et al., 2017; Jimenez et al., 2013). In this case, spontaneously established vegetation usually arises from topsoil seed sources (i.e. seed banks and propagules) and seed rain from the closest neighborhood (de la Riva et al., 2011; Mola et al., 2011). Over time, early established plants would modify soil properties, such as organic matter content, nutrient cycling, and water availability among other factors (Eviner and Hawkes, 2008; Jimenez et al., 2013), affecting the distribution and abundance of late-arriving plants (de la Riva et al., 2011). Thus, it is important to understand the characteristics of early established vegetation structure and composition on newly created road habitats (i.e. roadcuts and embankments) in order to gain insights into possible strategies for the restoration of plant communities similar to those of adjacent ecosystems. Understanding plant communities establishment and the environmental factors affecting them is a fundamental research area of restoration ecology (Bochet et al., 2007), with special importance for the reduction of the negative impacts of linear infrastructures by providing ecological restoration solutions that respond to site-specific needs (Martín-Sanz et al., 2015).

A variety of ecological filters such as environmental factors and soils regulate plant species establishment, composition, and structure (Tilk et al., 2017). Steepness of slopes is one of the main determinants of plant colonization and vegetation development in new road habitats (Feng et al., 2016; Paschke et al., 2000). For example, Bochet and García-Fayos (2004) reported that vegetation was not dense on roadcuts with slope angle >45°, which limited the water interception capacity and consequently increases soil runoff. Soil type and slope position can also influence soil fertility and humidity, consequently affecting vegetation abundance, composition, diversity (Hart and Chen, 2006; Müllerová et al., 2011), and indirectly slope stability. Therefore, one of the alternatives to advance vegetation colonization of road habitats has been the use of technical revegetation practices (i.e. topsoil spreading and hydroseeding) (Alday et al., 2010), mainly aimed at swiftly providing high plant cover on disturbed slopes to minimize soil erosion (Bochet and García-Fayos, 2004). However, the technical reclamation efforts usually do not give expected results in terms of fast and stable vegetation covers (Martín-Sanz et al., 2015). Therefore, a cheaper alternative could be to relay in natural successional process in sites where the conditions are optimal. For this, surrounding landscape is one of the key factors influencing species colonization, and therefore, composition and distribution. Douda (2010) suggested that plant species can spread quickly in areas with high connectivity (i.e. road borders), whereas plant dispersal may be limited in isolated areas. Hence, the influence of these environmental factors on the development of plant communities after road impacts are fundamental for future science-based restoration works (Wang et al., 2016). However, the real importance and influence of environmental factors in Western Asian ecosystems have not been explored.

Different studies about roadside and road construction have already reported changes in plant community composition according to the level of road improvement (paved or unpaved road) (Gelbard and Belnap, 2003), frequency of vehicle traffic (Sharma and Raghubanshi, 2009), or method of technical revegetation applied (Paschke et al., 2000). However, very few studies have described the patterns and distribution of vegetation colonization and establishment on different road habitats (roadcuts and embankments; but see (Feng et al., 2016). Despite the increasing importance of roadside vegetation restoration, knowledge about plant species successional processes or compositional differences in different new habitats created during road construction is currently limited in East Asia. For example, in Korea, previous road restoration studies have only focused on describing alterations in vegetation after a forest road construction (Han et al., 2018; Kim and Lee, 2001); however, attention has not been placed on how and what new plant communities are assembled in perturbed areas. On the contrary, in China, works describing the impacts of road and railway construction on vegetation, and the alteration of soil properties and vegetation development on different slopes have been widely examined (Chen et al., 2003; Feng et al., 2016). Furthermore, in Japan, only works describing the effects of roads on alpine and subalpine plant species distribution were conducted (Takahashi and Miyajima, 2010). In any case, only few studies in East Asia have analyzed roadcuts and embankments as important factors affecting naturally established vegetation. This analysis is fundamental for planning revegetation programs for similar disturbed areas using science-based methods.

To increase the effectiveness of revegetation works in road slopes, it is crucial to describe whether the habitats produced by road activities (e.g., roadcuts and embankments) are more easily colonized by native species or exotic invasive plants. This could be the first step in the identification of colonization potential of plants in South Korean road habitats, being the information gathered fundamental to design a science based future restoration measures (Nunes et al., 2016). Thus, our study explicitly defined the differences in species composition and diversity between four roadways and three habitat types (i.e. embankments, plain areas, and roadcuts) in South Korea. In addition, colonizing native and exotic plants species will be described. We hypothesized that exotic plants will be more abundant on embankments which contains soil layers taken from degraded areas and with high potential of sustaining an invasive plant seed bank. In contrast, native plant species will be more abundant on plain areas and roadcuts, as these areas were not top-soiled and thus would be colonized by the surrounding native plants (Bochet and García-Fayos, 2004; Münzbergová and Herben, 2005). The specific questions of this study were (1) there were differences in species composition between roadways and habitat types?, (2) What are the main environmental factors affecting species composition (i.e. soil type, soil slope and surrounding landscape)? (3) Which are the indicator species of each habitat type? and (4) what are the diversity differences and the number of native or exotic species between different habitats?

2. Method

2.1. Study area

The study was conducted in four similar road construction areas, Gyeonggi-do (36–38° N, 126–127° E), South Korea: Jeongok-Youngjung roadway (JG) 13.9 km (20 sites), Seolma-Gueup roadway (SM) 8.0 km (23 sites), Singal roadway (SG) 5.1 km (26 sites), Samga-Daechon roadway (DC) 7.4 km (32 sites; Fig. 1). Jeongok-Youngjung and Seolma-Gueup roadways are located in the northern part of Gyeonggi-do province, while Singal and Samga-Daechon roadways are in the southern part. These sites were surrounded by mountains and croplands where *Pinus* spp., *Quercus* spp., and *Robinia* spp. were abundant, and the most widespread soils, classified by Korean Soil Information System (National Institute of Agricultural Sciences, https://soil.rda.go.kr) as Andisols, Entisols, and Inceptisols on metamorphic rock and acidic rock. The climate is temperate with a mean annual temperature of 12.5 °C and a mean annual precipitation of 1308 mm from 1981 to 2010 (Korea Meteorological Administration, 2018).

2.2. Sampling design

First, we classified the road habitats into three types considering their characteristics: i) roadcuts (constructed by excavation), ii) embankments (by heaping and compacting materials), and iii) plain areas (flat and bare areas) (Jimenez et al., 2013; Martín-Sanz et al., 2015). We then selected over the four roadways all possible different habitats available per roadway taking environmental variation into account: a total of 49 roadcuts, 27 plain areas, and 25 embankment habitats were selected (i.e. JG: 3 roadcuts, 5 plains, 12 embankments; SM: 9 roadcuts, 10 plains 4 embankments; SG: 19 roadcuts, 5 plains, 2 embankments; DC: 18 roadcuts, 7 plains, 7 embankments; 101 total). In each habitat, we also recorded the slope angle, topsoil type (i.e. sand, cobble, or rock) and adjacent surrounding landscape (i.e. forest, crop land, or road).

The vegetation sampling was conducted along each roadway during the spring and summer of 2017. Vegetation sampling was carried out using five quadrats of 1 m^2 per each of the 101 sites (1 × 1 m^2; n = 505). The quadrats were randomly located across each site sampling area (ca.100 m^2). The cover (%) of all the present species in each quadrat was visually estimated. Species identification and nomenclature followed 'The Plant List (http://www.theplantlist.org)' and 'The Korean Plant Names Index (KPNI) database (www.nature.go.kr/ekpni/SubIndex.do)'.

2.3. Data analyses

Statistical analyses were performed in the R software environment (R Core Team, 2018), using the "vegan" package for multivariate and diversity analyses (Oksanen et al., 2017), "indicspecies" package for indicator species analysis (Cáceres and Legendre, 2009), and the generalized linear models (GLM) function for comparison of richness, evenness, and the number of exotic and native plants among roadways and habitats.

Vegetation community data was analyzed using both multivariate and univariate methods. First, to describe the differences in plant species composition between habitat types and roadways, we used permutational multivariate analysis of variance performed with the function "adonis" (Oksanen et al., 2017). Here, the sampling structure was included limiting randomizations within each habitat and roadway. In addition, differences in species composition were tested using Bray-Curtis distance (Ross et al., 2012). Species cover values were initially log-transformed (log(cover+1)) to reduce the influence of rare species. Afterwards, we performed a NMDS using the Bray-Curtis dissimilarities, and the habitat and site standard deviational ellipses ('ordiellipse' function) were plotted in the ordination space to clearly describe their compositional differences.

Second, indicator species analysis was used to identify the most abundant or frequent species in the roadways and habitats. Each species was associated with a vector of indicator values for each group and significance of indicator value was tested by permutation of the raw data matrix (De Nicola et al., 2017). Third, Pielou's evenness, species

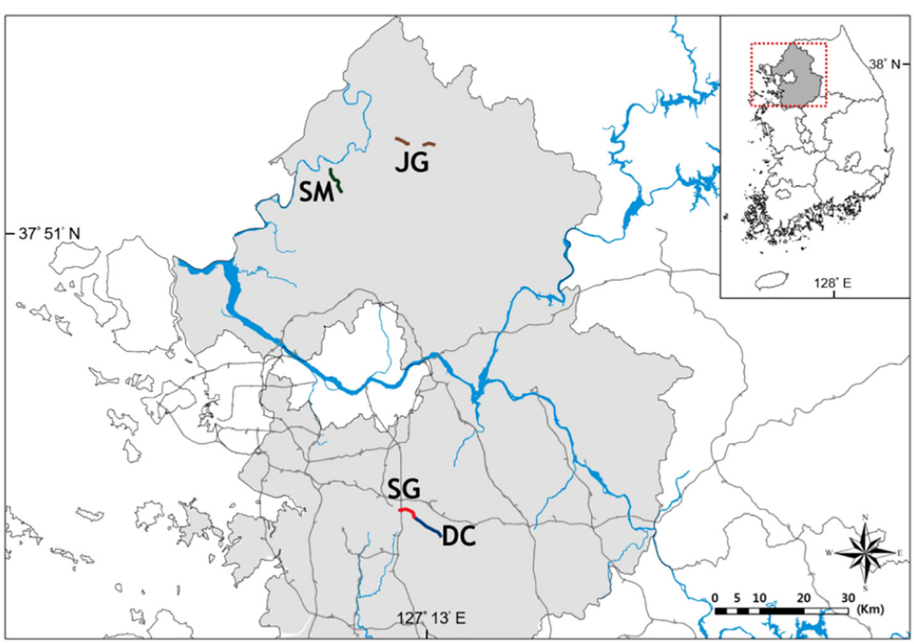

Fig. 1. Location of surveyed roadways in South Korean peninsula. Northern region: JG, Jeongok-Youngjung; SM, Seolma-Gueup; Southern region: SG, Singal; DC, Samga-Daechon roadways.

richness, and the number of exotic and native species by habitat or roadway were compared using GLM with Gaussian or Poisson error distributions (Hrivnák et al., 2015).

3. Results

A total of 138 plant species from 32 families were found: 73 plant species in SM, 71 in JG, 73 in SG, 82 in DC. Splitting these values by habitats: 91 plant species were identified in the embankments, 92 in the roadcuts, and 100 in the plain areas. Among the species identified, there were 82 native, 50 exotic, and six cultivated plants, representing 41% of total species. The most abundant species were *Medicago sativa* (relative coverage 10.9%), *Artemisia princeps* (6.7%), *Ambrosia trifida* (6.2%), *Humulus scandens* (4.9%), *Setaria viridis* (4.8%), *Coreopsis lanceolate* (4.5%), *Lespedeza bicolor* (4.3%). Three out of the seven most abundant species, *Medicago sativa*, *Ambrosia trifida*, and *Coreopsis lanceolate*, were non-native species.

3.1. Plant compositional differences by roadways and habitat types

There was a significant interaction between roadways and habitats types on plant species composition, although only 5% of compositional variance was explained (PMAV; $F = 5.54$; $p = 0.001$; $r^2 = 0.05$). In contrast, 12% and 6% of the species compositional differences were produced when roadways and habitat type factors were considered individually ($p = 0.001$). NMDS ordination (stress: 0.19; Fig. 2) and standard deviational ellipses showed clearly the interaction effect between roadways and habitats types. Considering embankments, northern JG and SM roadways were grouped at the negative end of axis 1 with no significant differences between them (Fig. 2b), and southern DC and SG embankments were located at the positive end of axis 1, but differed from each other significantly (i.e. SG is located at axis-2 positive end while DC is located at the negative end, Fig. 2b). For the plain habitats, there were only two clear different groups that fit with the northern and southern regions; JG-SM roadway was located at the negative end, and DC-SG group was located at the positive end (Fig. 2c). In contrast, the roadcut habitats showed patterns that were completely different from those of embankments and plain habitats. JG roadcuts were located in the lower left part of the ordination, being significantly different from SG-DC groups that were grouped at the right upper side, whereas, SM group was in a central position, and not significantly different from the rest of the habitats (Fig. 2d). Overall, two roadway groups were clearly differentiated; JG-SM located at the northern region of the province and the southern sites, DC-SG, which were separated along the axis 1. Among the most important species identified, *Ambrosia trifida*, *Zoysia japonica*, *Centaurea cyanus*, *Oenothera biennis*, and *Humulus scandens* were associated with JG site; *Ambrosia trifida*, *Humulus scandens*, *Setaria viridis*, *Lolium multiflorum*, and *Artemisia princeps* were associated with SM site; *Medicago sativa*, *Lespedeza cuneata*, *Lotus corniculatus*, *Lespedeza bicolor*, and *Indigofera pseudotinctoria* were associated with SG site; and *Artemisia princeps*, *Coreopsis lanceolate*, *Lespedeza bicolor*, *Pueraria montana* var. *lobate*, and *Erigeron annuus* were associated with DC site (Fig. 2a).

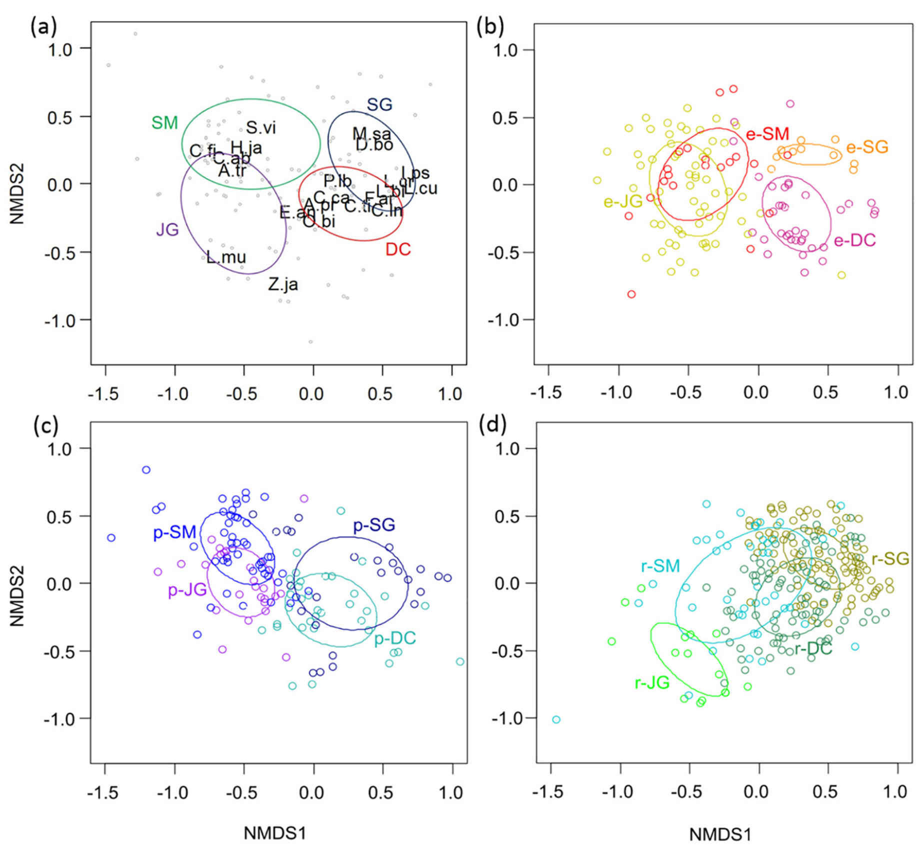

Fig. 2. NMDS ordination for the first two axes of compositional differences among four roadways and three habitat types of South Korean peninsula, illustrating: (a) species biplot where only species with >75 of sum of log-scaled cover are shown. Less important species are represented as gray circles. Species codes are A.tr, *Ambrosia trifida*; A.pr, *Artemisia princeps*; C.ab, *Chenopodium giganteum*; C.ca, *Erigeron canadensis*; C.fi, *Chenopodium ficifolium*; C.ln, *Coreopsis lanceolate*; C.ti, *Coreopsis tinctoria*; D.bo, *Dendranthema boreale*, E.an, *Erigeron annuus*; F.ar, *Festuca arundinacea*; H.ja, *Humulus scandens*; I.ps, *Indigofera pseudotinctoria*; L.bi, *Lespedeza bicolor*; L.cr, *Lotus corniculatus*; L.cu, *Lespedeza cuneate*; L.mu, *Lolium multiflorum*; M.sa, *Medicago sativa*; O.bi, *Oenothera biennis*; P.lb., *Pueraria montana* var. *lobata*; S.vi, *Setaria viridis*, Z.ja, *Zoysia japonica*. (b) Ordination biplot with deviational ellipses for embankments, (c) ordination biplot with deviational ellipses for plains, and (d) ordination biplot with deviational ellipses for roadcuts. The circles in (b), (c), and (d) show the sampling sites, and roadways are represented as JG, SG, DC, and SM.

3.2. Environmental effects on species composition and indicator species analyses

Surprisingly, soil type, soil slope, and surrounding landscape did not show a significant effect ($p > 0.05$) on species composition. Generally, environmental variables contributed to a residual amount of compositional variance (i.e. each variable contributes to <3% of the variance in the species data). Furthermore, the indicator species analysis involved all the 48 species as indicator species for the different roadways and habitats (Table 1). Twenty-four (50%) were native species, 22 exotic species (46%), and two (4%) were cultivated species. Exotic species were found in all the roadways and habitat types (Table 2). Unexpectedly, in the DC, even considering the different habitats, all indicator species were exotic plants (5 exotic species/5 indicator species, 100%), followed by JG (7/14, 50%), SG (5/14, 35.7%), and SM (5/15, 33.3%). Overall, the main indicator species types are annual/biennial species (29/48, 60.4%), followed by perennial forbs (14/48, 29.2%), and woods/shrubs (5/48, 10.4%).

Table 1
Indicator species in four roadways and three habitat types in South Korean peninsula. An asterisk represents exotic plant. AB, annual or biennial; P, perennial; W, wood or shrub. Roadway acronyms: JG, Jeongok-Youngjung; SM, Seolma-Gueup; Southern region: SG, Singal; DC, Samga-Daechon roadways. In the SM roadway there were not indicator species for Roadcut habitats, so they are missed form the table. Stat is the association statistic of the permutational test from the indicator species analysis, higher stat value means that the species is more strongly associated with the habitat.

Roadway	Habitat	Species	Life Span	Stat	p-Value
DC	Embankment	*Coreopsis lanceolate**	P	0.453	0.001
DC	Plain	*Erigeron annuus**	AB	0.480	0.001
		*Silene armeria**	AB	0.324	0.039
DC	Roadcut	*Amorpha fruticose**	W	0.359	0.004
		*Coreopsis tinctoria**	AB	0.304	0.027
JG	Embankment	*Brassica napus*	AB	0.453	0.004
		Fagopyrum esculentum	AB	0.443	0.002
		*Trifolium pretense**	P	0.349	0.011
		Alopecurus aequalis	AB	0.289	0.025
JG	Plain	*Ambrosia trifida**	AB	0.493	0.001
		Chenopodium giganteum	AB	0.416	0.003
		*Ambrosia artemisiifolia**	AB	0.393	0.008
		*Carduus crispus**	AB	0.385	0.003
		Hemistepta lyrata	AB	0.358	0.004
		*Rumex crispus**	P	0.282	0.036
		Stellaria aquatica	P	0.263	0.045
JG	Roadcut	*Centaurea cyanus**	AB	0.912	0.001
		Zoysia japonica	P	0.616	0.001
		*Lolium perenne**	P	0.492	0.001
SG	Embankment	*Medicago sativa**	P	0.683	0.001
		*Lactuca scariola**	AB	0.399	0.003
		Bidens bipinnata	AB	0.334	0.006
		Metaplexis japonica	P	0.269	0.045
SG	Plain	*Erigeron canadensis**	AB	0.611	0.001
		Lespedeza cuneata	P	0.387	0.002
		Albizia julibrissin	W	0.381	0.004
		Lespedeza bicolor	W	0.373	0.008
SG	Roadcut	*Indigofera pseudotinctoria*	W	0.466	0.001
		*Taraxacum campylodes**	P	0.323	0.011
		*Lotus corniculatus**	P	0.322	0.016
		Artemisia annua	AB	0.309	0.016
		Chrysanthemum burbankii	P	0.285	0.039
		Brucea javanica	W	0.281	0.022
SM	Embankment	*Persicaria senticosa*	AB	0.452	0.001
		Lespedeza daurica	P	0.445	0.001
		Humulus scandens	AB	0.433	0.003
		*Lolium multiflorum**	AB	0.376	0.006
		Equisetum arvense	P	0.333	0.021
		*Thlaspi arvense**	AB	0.277	0.024
SM	Plain	*Setaria viridis*	AB	0.473	0.002
		*Amaranthus retroflexus**	AB	0.392	0.005
		Persicaria perfoliata	AB	0.384	0.004
		*Chenopodium ficifolium**	AB	0.364	0.009
		Persicaria nodosa	AB	0.355	0.016
		*Chenopodium album**	AB	0.339	0.017
		Commelina communis	AB	0.293	0.032
		Echinochloa crus-galli	AB	0.283	0.028
		Portulaca oleracea	AB	0.283	0.037

Table 2
Number of exotic and native indicator species in four roadways of South Korean Peninsula. Roadway acronyms: JG, Jeongok-Youngjung; SM, Seolma-Gueup; Southern region: SG, Singal; DC, Samga-Daechon roadways.

Roadway	Habitat	Exotic indicator species	Native indicator species
DC	Embankment	1	0
	Plain	2	0
	Roadcut	2	0
JG	Embankment	1	2
	Plain	4	3
	Roadcut	2	1
SG	Embankment	2	2
	Plain	1	3
	Roadcut	2	3
SM	Embankment	2	4
	Plain	3	6
	Roadcut	–	–

3.3. Diversity and exotic species presence between roadways and habitats

There was an interactive effect of roadways and habitats in plant species richness ($F_{[6,89]} = 9.01$, $p < 0.001$; Fig. 3a). Here, only the SG roadway showed no significant differences in richness among habitats (Fig. 3a). On the contrary, roadcut showed a significantly higher richness value in DC and a significantly lower richness value in JG and SM. The species richness of embankment at DC was significantly lower than that at SM, and the richness of roadcut at DC and SG was significantly higher than those at JG and SM. The evenness values were high for all roadways and habitats oscillating between 0.8 and 0.9. Furthermore, there was a roadway and habitat interaction on evenness ($F_{[6,89]} = 4.09$, $p < 0.05$; Fig. 3b). Here, SG and SM roadways showed no significant differences in evenness among the habitats, whereas roadcuts at DC showed significantly greater evenness values. On the contrary, roadcut showed higher evenness than embankment at JG. The roadcuts' evenness showed the highest variation among the roadways; however, the embankments' and plains' evenness were not different among the roadways.

The exotic species richness for all sites ranged from 1 to 14 species (Fig. 4a). Although only at DC, there were differences in the richness of the exotic species of the habitats, with roadcuts showing higher exotic richness. The exotic species richness of DC roadcuts was greater than those of JG and SM. In the other two habitats (plain areas and embankments), there was no difference in the exotic richness of the roadways (Tukey test, $p > 0.05$). On the contrary, native species richness ranged from 0 to 15 species (Fig. 4b). JG and SM showed the lowest native species richness on roadcuts, whereas embankments showed similar native species richness on other roadways. DC and SG had greater native species richness on roadcuts than JG and SM; however, there were no differences in the native species richness of DC and SG among the habitat types.

4. Discussion

Although some studies have reported the establishment and diversity patterns of plant species in new road habitats from various regions worldwide (Bochet et al., 2007; Martín-Sanz et al., 2015; Wang et al., 2016), the colonization potential of these new habitats by native or exotic species in eastern Asian countries has not been investigated, especially in South Korea. Here, our results showed that the composition of established plant species was influenced by the interaction between roadways location and habitats types. In addition, this interaction also affected plant richness and evenness trends. Surprisingly, environmental variables such as soil, slope, and surrounding landscape types had less influence on plant species composition than expected, with a

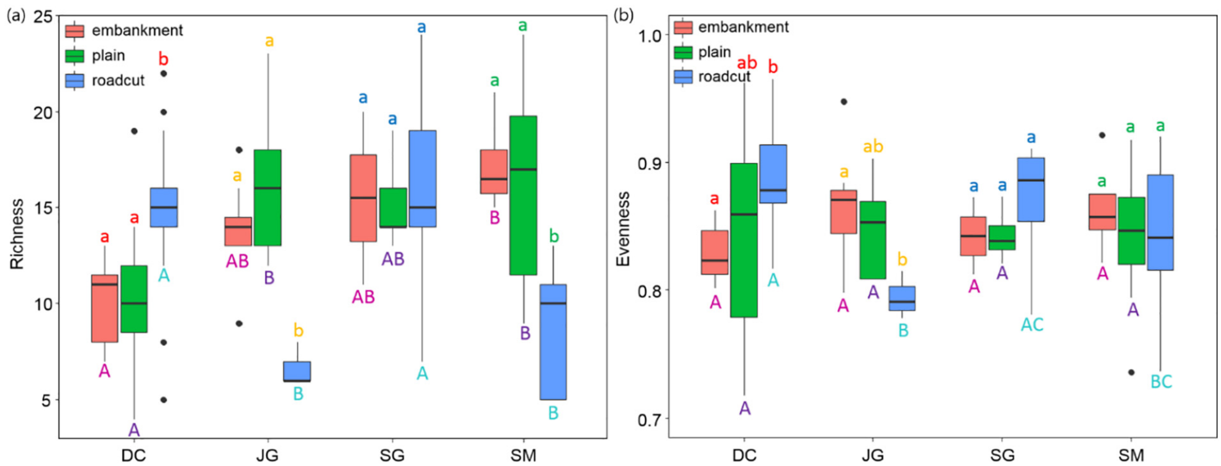

Fig. 3. Boxplots for (a) plant richness and (b) evenness in different habitats per roadway in South Korean peninsula. Different small letters indicate significant post-hoc differences among habitats in the same roadways and large letters indicate significant differences among roadways of the same habitats (Tukey test, $p < 0.05$).

residual amount of explained variation. Nevertheless, 48 species were described as indicators of different roadways and habitat types, and unfortunately, 50% of them were invasive or cultivated species. These results suggest that different regional-dependent processes, such as northern vs. southern roadways, interact with newly created habitats (i.e. roadcuts, embankments, and plane areas) to produce complex patterns of plant species colonization and composition. Thus, ecological restoration solutions should focus on site-specific needs, with consideration to the differences between northern and southern roadways. In addition, the restoration solutions should be based on the plant communities spontaneously established in these degraded areas. The high proportion of exotic plant species found and their great contribution to the total diversity described in this work, highlights the capacity of invaders to colonize road-habitats, emphasizing the importance of planning and designing ecological restoration strategies based on identified native species for these areas.

4.1. Species compositional differences by roadways and habitats

Recent works over disturbed habitats have demonstrated that colonizing plant species and the communities that they formed are related to propagules abundance and the dispersal strategy (species pool) of the adjacent undisturbed habitats (Rentch et al., 2005). Thus, it is expected that nearby roads have similar patterns of species composition and diversity (Martínez-Ruiz and Fernández-Santos, 2005; Tikka et al., 2001). Here, our results agreed with previous reports as overall plant species composition was similar on geographically close roadways, such as JG and SM located in the northern part of Gyeonggi-do, or the DC and SG roadways located in the southern part. de la Riva et al. (2011) suggested that species composition is determined by species availability from the regional pool and surrounding matrix. Thus, having similar source of propagules is one of the main factors conditioning spontaneously established plant communities in road habitats. Therefore, restoration plans or actuations for new degraded roadways should take into consideration the regional-level species-pool to identify their potential as propagule donors and to know the type of species that would be able to colonize the area.

When road habitats were analyzed, regional differences were clear, especially in embankments and plain areas in which northern versus southern differences prevail. However, it is interesting to mention that there were also compositional differences in embankments at the southern roadways. Embankments are formed by heaping and compacting of soil materials, which may contain viable seed banks (Jimenez et al., 2013) that can condition the spontaneous development of vegetation communities (Mola et al., 2011). This affects the distribution and abundance of late-arriving plants by reducing suitable sites for colonization or outcompeting them (de la Riva et al., 2011). In our study, considering that southern roadways only showed differences in the composition of the embankment habitats (Fig. 2), it seemed that DC or SG embankments were top-soiled with soils hosting seedbanks from different sources, because the local colonization process would create similar communities to those in roadcuts and plain areas. The use of soil with removed top layers for the restoration of disturbed road areas is a necessary measure to reduce the formation of undesirable plant communities or non-native species invasions (Alday et al., 2011).

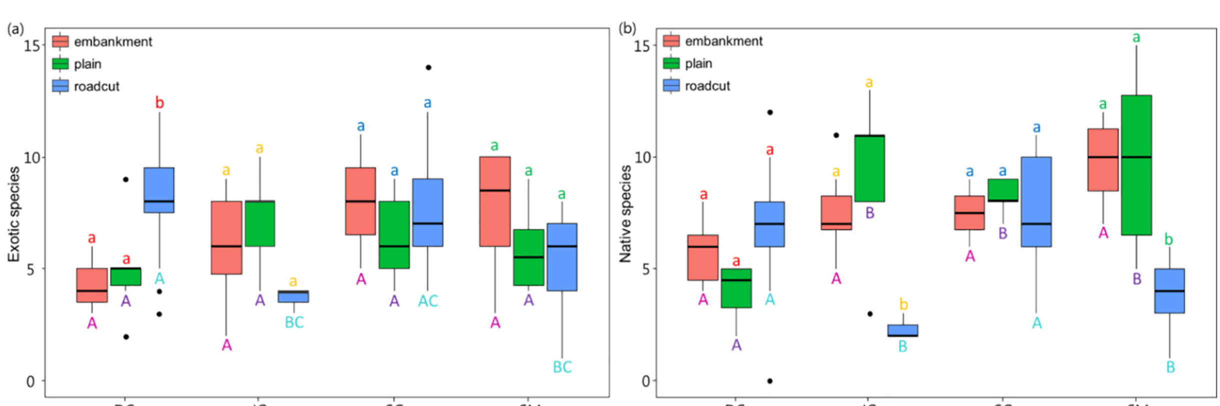

Fig. 4. Boxplots for (a) exotic species richness and (b) native species richness in the different habitats per roadway in South Korean peninsula. Different small letters indicate post-hoc significant differences between habitats in the same roadways and large letters indicate significant differences between roadways of the same habitats (Tukey test, $p < 0.05$).

Roadcuts are the hardest habitats created after road construction, characterized by steeper slopes and lack of formed soils (Mola et al., 2011) which restrict the spontaneous establishment of surrounding vegetation to species that are adapted to these limiting conditions. Therefore, roadcuts species composition is usually more similar within roadcuts than among the flora of adjacent regional areas (Bochet et al., 2007). Our results agreed with these patterns as SM, SG, and DC roadcuts showed similar species composition and only JG showed slightly different trend. Identifying plant species that passed the ecological filters and were able to establish on roadcuts in our study could be useful in future restoration studies on similar roadcuts independently of being located at the northern or southern part.

4.2. Main environmental factors effecting species composition

Surprisingly, the environmental factors analyzed in this study, such as soil type, slope, or surrounding landscape type, did not have a significant effect on roadways colonizing plant species composition. These results might be due to i) inadequate selected variables or ii) other more restrictive environmental or ecological filters for vegetation establishment. In the case of selected variables, soil types based on the textures of different habitats did not affect species composition, and the four roadways seemingly had similar bedrock or contain soil from embankments or roadcuts from roadways with similar properties. Unfortunately, the soil physico-chemical characteristics were not analyzed in this study; thus, a new study should target the effect of soil properties in the described established patterns. This is necessary because similar restoration studies have demonstrated that soil limits seedlings establishment and growth (Alday et al., 2011; Arenas et al., 2017b). Surrounding landscape was categorized into forest, cropland, and road to examine their influence on vegetative colonization. However, it seemed that even in sites surrounded by road landscapes, the plant colonization processes from adjacent areas were not limited by vegetation type and even by road slopes. This indicates that established plant community and diversity in these roadways were apparently unaffected by the selected abiotic factors, probably because they were not as restrictive for plant establishment in these areas as previously though. In any case, further research should be done in these areas in order to clarify the effects of abiotic and soil factors on vegetation composition and plant dispersal traits, as well as the resistance of established plant communities to water stress (Bochet et al., 2007; de la Riva et al., 2011; Jimenez et al., 2013; Mola et al., 2011).

4.3. Indicator species in roadways and habitats

Indicator species analysis showed that 48 species exhibited a significant affinity to one habitat of each roadway, although, a great number of exotic species were selected as indicators especially in DC roadway. Three out of 14 exotic invasive plants described as indicator species (i.e. *Ambrosia artemisiifolia*, and *Ambrosia trifida* in the JG, *Lactuca scariola* in the SG) were designated by Ministry of Environment of Korea as challenging, producing important ecological impacts. At the same time, the genus *Lolium* (*Lolium perenne* on the roadcut of the JG and *Lolium multiflorum* on the embankment of the SM) has been known as a highly competitive and aggressive species (Hofmann and Isselstein, 2004; Matesanz et al., 2006), and especially, *Lolium perenne* grows vigorously near roads (Spellerberg, 1998). Thus, invasive species on new habitats should be controlled to prevent their spread and dispersal.

Disturbances provoked by road construction provide the opportunity for exotic species to invade new plant communities (Barbosa et al., 2010). Road construction creates safe areas for exotic invasive plants by removing native species and its seed bank and adding new soil layers, thereby facilitating germination and establishment (Barbosa et al., 2010; Trombulak and Frissell, 2000). Some exotic invasive plants are able to outperform native species in low-nutrient soil environment (González et al., 2010). They produce propagules at much faster rates than native species, with evolved strategies and adaptations to colonize the newly created habitats (Barbosa et al., 2010). In addition, imported road-building materials, vehicles, and people may convey exotic plant seeds into roadside areas (Greenberg et al., 1997; Paiaro et al., 2011). In this study, DC and JG roadways had early stage areas of unstable soil, which are less stable environment for the establishment of native species communities, favoring the dominance of exotic species.

With regards to the types of indicator species identified, we found that annual/biennial species were the most established species on the roadsides, and perennials and woody plants were not found on the sites. Perennial forbs are known to be able to persist on harsh roadways; however, the greatest limit to the establishment and growth of perennials and woody species on the newly created habitats is lack of appropriate soils with the associated limitations such as lack of nutrients, soil depth, or soil symbionts (Paschke et al., 2000). Most mid- to late-successional perennials in the disturbed sites depend on appropriate soils for establishment and survival (Paschke et al., 2000; Walker and Smith, 1997). However, the survey of degraded sites over a 14-year period showed that successional trajectories of species richness and abundance demonstrated significant declines of annuals/biennials or short-lived perennials when soil conditions were improved, due to suppression by perennials and shrub species (Foster and Tilman, 2000). In view of this pattern, it is clear why annual/biennial indicator species were the most dominant in the disturbed habitats of the roadways. Thus, longer time frames will be needed to test if successional trends or arrested successions are happening in the study sites (Lupardus et al., 2019).

4.4. Diversity differences between roadways and habitats

Overall, the richness and evenness of the exotic and native species of the roadcuts at DC and SG were higher than those at JG and SM. This result resembles species compositional trend described previously, with clear differences between northern and southern roadways. The result also highlights the importance of regional species pool on richness and evenness. Considering the habitats, our results for the roadcuts showed a similar trend, in which plant richness and native plant richness at JG and SM, northern roadways, was significantly lower than those at DC and SG roadcuts, at southern roadways. In contrast, richness local effects were not maintained when embankment and plain areas were analyzed. This agreed with the study of Rentch et al. (2005) which reported uniform species richness and evenness in relation to different road habitats.

In our study, northern roadcuts were seemingly trickier to restore as they were colonized by less number of species, although compositionally, the results were like those of other roadways. The severity of erosion processes (i.e. rill erosion, gully erosion, and mass movement) (Bochet and García-Fayos, 2004) may restrict species colonization on northern roadcuts. In any case, roadcuts are known to restrict species establishment because of the inherent characteristics of each site (e.g., soil condition, surrounding vegetation, seed bank, and microsite) (Münzbergová and Herben, 2005).

4.5. Management implications

Our findings highlight roadside habitat and roadways location as important factors controlling plant composition and diversity during road construction in South Korea, suggesting that roadside habitats differ in their susceptibility to plant colonization. In this regard, an important fraction of the regional species pool can disperse and settle on newly created habitats on both northern and southern roadways. Therefore, restoration plans on these areas should take these regional or local conditions into consideration for improved outcome. At the same time, as a restoration strategy for the studied sites and similar degraded sites, the surrounding native vegetation should be kept close to the degraded sites to promote natural colonization processes at low-cost (Karim and Mallik, 2008; Tormo et al., 2007). Natural colonization has the advantage of increasing local diversity in newly created sites (Arenas et al., 2017a; Prach and Hobbs, 2008). Unfortunately, the colonization of the degraded sites by exotic species, as we found in all habitats of DC roadway, is a restoration problem that should be addressed (Alday et al., 2013). The continuous colonization of exotic species in newly disturbed habitats modifies the functions, services, and landscape of the natural ecosystem (Barbosa et al., 2010), and thus, the already established exotic species should be directly managed in the study sites. During road construction, the invasive spread of exotic species should be controlled by local government office and construction corporation. Overall, our results also showed higher species richness on embankments and plain areas. According to the Concostrina-Zubiri et al. (2019), steeper slopes and coarser soils are seemingly found more frequently in roadcuts. Thus, when restoration or revegetation actions are necessary, roadcuts should be managed more carefully than embankment and plain areas.

In the road environments of South Korea, at least 175 exotic species out of 321 exotic plants described in the country can be found colonizing road habitats (Mason Heberling et al., 2017). This wide colonization of roadside degraded sites favors the rapid migration of exotic plants across the construction areas (Chu et al., 2017). Here, our study can give insights for vegetation restoration using native species, i.e. the species described as good colonizers in our work, as well as, our results suggest establishing a customized vegetation restoration plans according to the roadside habitats. Finally, it is important to take into consideration that the aforementioned suggestions have been derived from the findings of a monitoring program within ongoing roadways colonization schemes. Therefore, the effectiveness of these recommendations, from a restoration point of view, needs to be tested in future experiments.

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Declaration of competing interest

There are no potential conflicts of interest to declare.

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