Original article

Drove roads: Keystone structures that promote ant diversity in Mediterranean forest landscapes

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A R T I C L E   I N F O

A B S T R A C T

Drove roads are the traditional corridors used by pastoralists for seasonal movements of livestock (transhumance). They cover a considerable land area in Mediterranean countries and, although they are an obvious source of landscape diversity, their influence on the diversity and composition of animal assemblages has not been documented. Ant communities were studied on four active drove roads, two in forests (submediterranean and conifer) and two in open environments (croplands and rangelands). They were compared with the respective matrix communities and their contribution to local species richness was evaluated. The effects were heavily dependent on the open or closed nature of the matrix. In forest environments, drove roads increased ant species richness at the local scale, acting as clear keystone structures. Their species richness and functional diversity were highest on the fine scale, species composition was different, and a slight edge effect in the matrix was detected. In contrast, drove roads had little or even a negative effect in open environment locations. We conclude that drove roads have a high conservation value for ants in Mediterranean forest environments, in addition to their importance as reservoirs of plant biodiversity and generators of ecological goods and services.

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1. Introduction

Drove roads, also known as stock routes, are one of the most characteristic components of traditional landscapes in Mediterranean countries (Ruiz and Ruiz, 1986; Mangas Navas, 1992; Merino García and Alier Gándaras, 2004). Active drove roads stand out in the landscape as well-defined strips up to 100 m in width with a savannah-like grassland appearance, in some cases running for several hundred kilometres. They are reserved for and ecologically modeled by transhumance, a traditional type of pastoralism consisting on the seasonal movement of livestock between summer and winter pastures. In Spain, drove roads cover nearly 1% of the country's land area, with a total length of about 125,000 km (Mangas Navas, 1992; Merino García and Alier Gándaras, 2004). Due to their grid-like distribution, most of the country's land area is in contact with or near a drove road (Azcárate et al., 2012). Drove roads are at least several centuries old, and may have originally been based on the migratory routes of wild ungulates (Manzano and Casas, 2010). Because of their enormous area, long-term persistence, impact on the landscape structure and capacity to host herbivore migrations, drove roads can have played a major ecological role in the Mediterranean Basin. The current crisis in extensive grazing has led to the abandonment of transhumance and grazing uses of drove roads (Ruiz and Ruiz, 1986; Ruiz, 2001), causing a loss of their differentiation from the surrounding ecological matrix. Their influence on populations and communities may thus disappear before they are identified and studied.

The few published ecological studies of drove roads have focused on their effects on plant communities. Drove roads have traditionally been regarded as a good example of ecological corridors for plant species (review in Bunce et al., 2006), although no experimental evidence supported this view until Manzano and Malo (2006) detected epizochorous seed dispersal over distances of up to 400 km. More recently, the effects of drove roads on landscape patterns, species composition and functional diversity of plant communities have been measured (Azcárate et al., 2012), showing that drove roads are a source of spatial heterogeneity and a reservoir for many plant species in non- or moderately-grazed habitats.

Drove roads could also have a noticeable effect on the diversity and composition of animal assemblages. Active drove roads maintain patches of open grassland in non-grazed environments such as forests, and hence increase spatial heterogeneity. Spatial heterogeneity and diversity of several animal species groups are often

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(but not always) correlated (Duelli, 1997; Atauri and de Lucio, 2001; Szczepko et al., 2012). It has been argued that each animal species group depends on a specific structural aspect of the vegetation whose presence or quality can be detected at a certain spatial scale (Tews et al., 2004). At that scale, biodiversity is favoured by the occurrence of "keystone structures", characterized by their ability to provide resources, shelter or nesting sites to that species group. Examples of keystone structures at different spatial scales are tree cavities in forests (for insects, birds and mammals), trees in African savannas (for arboreal rodents, ungulates, raptors and other species groups) and temporary wetlands in agricultural fields (for carabid beetles) (Tews et al., 2004; Remm and Lohmus, 2011). If a key structure affects several species groups, or groups with a strong influence on ecosystem functioning, then its conservation is of crucial importance. Drove roads might then function as keystone structures by favouring rich groups of terrestrial species with relevant roles on ecosystem functioning, such as ants.

Ants are considered to be a focal group for the monitoring of terrestrial ecosystems (Underwood and Fisher, 2006; Crist, 2009). This is not surprising, given their ability to stockpile a considerable amount of primary and secondary production, interact with several organisms and act as ecosystem engineers (Folgarait, 1998; MacMahon et al., 2000; Crist, 2009). Literature shows that ants respond strongly to land management (Bestelmeyer and Wiens, 1996; Chen et al., 2011), and are sensitive to different levels of grazing (Read and Andersen, 2000; Boulton et al., 2005; Azcarate and Peco, 2012). Moreover, ants are widespread, moderately diverse and easy to sample (Alonso and Agosti, 2000; Andersen et al., 2004). Their role as indicators has improved with the development of the concept of functional groups to classify ants within species assemblages, as first proposed in Australia (Andersen, 1995), and then extended worldwide (Brown, 2000). More recently, the role of ants in ecosystem functioning has been studied by measuring their functional diversity (Bihn et al., 2010; Silva and Brandao, 2010) although this approach has still been little addressed, in contrast to other taxa.

The present study evaluates the role of drove roads as keystone structures. Specifically, our work analyzes the effects of drove roads on ant assemblages by measuring species richness, functional diversity and species composition on active drove roads and in the surrounding landscape matrices. Four sites were chosen in different traditional Mediterranean landscapes along a gradient of forest growth. We expected the effects to be dependent on the location, increasing with structural differences between the drove road and the ecological matrix.

2. Materials and methods

2.1. Study area

The study was done on the siliceous southern pediment of the Guadarrama Range (Madrid Autonomous Region, Central Spain, Fig. 1; Table 1). The four selected locations along a forest gradient were representative of the major landscape units in the area (Coniferous forest, Sub-Mediterranean forest, Rangeland and Cropland). All locations included a drove road with moderate grazing intensity and no sign of land disturbance by non-livestock agents. In all cases, the ecological matrix was well preserved and managed in a similar way to traditional land uses for at least the last 30 years.

2.2. Sampling design

In each location, we selected an approx. 2 ha drove road fragment of about 300 m—400 m long by 40—50 m wide. Three habitat
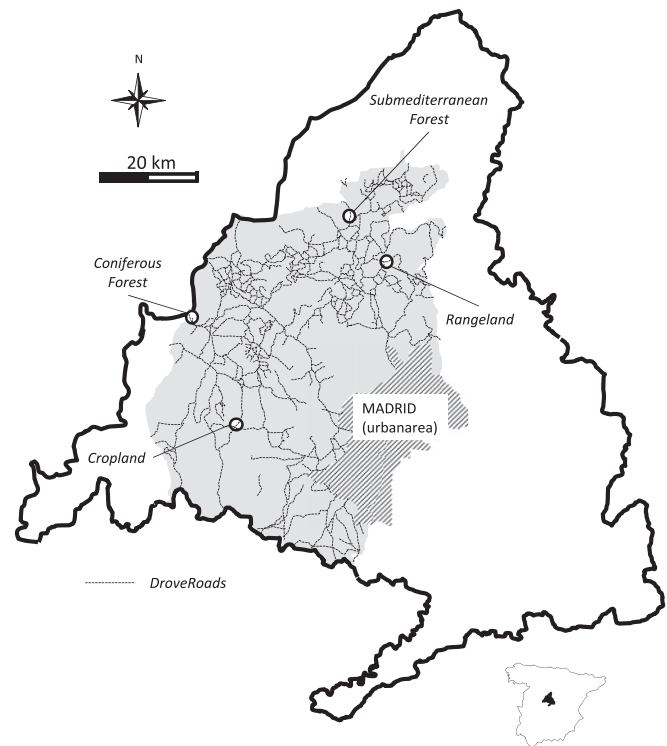

Fig. 1. Study area in the Madrid Autonomous Region (Spain). The map shows the study locations and the drove road network. The drove road distribution is taken from the official map in www.viaspecuariasdemadrid.org.

types were distinguished in each location: the drove road itself, the adjacent matrix and the distant matrix. The adjacent matrix was located between the edge of the drove road and a distance of 75 m, while the distant matrix was more than 200 m from the edge. Both types of matrices were structurally similar, but were considered separately to take into account potential edge effects in the adjacent matrix. The slope and aspect of the three habitat types (drove road, adjacent matrix and distant matrix) were similar in each location.

Sampling was performed in July 2010. Fifteen sampling units were randomly arranged in each location, five per habitat type. All sampling units of the same habitat type were included in the 2 ha area, set at least 25 m apart. One sampling unit consisted of (1) a set of three pitfall traps (2 cm diameter × 5 cm deep) forming a triangle with vertexes 1 m apart (for ground-dwelling species) and (2) a set of three baits in different trees less than 10 m apart (for arboreal species). The pitfall traps were filled with a mixture of 70% ethanol and 30% mono-ethylene glycol, and left in the field for 5 days. The bait, a combination of 1 cm^3 of honey and 1 cm^3 of tuna in oil, was placed at a height of 1.5 m on the tree trunk, then checked after 30 min. We recorded all ant species detected within 1 m of the bait in a 2-min observation. Each sampling unit was characterized by the complete list of species detected using both methods.

2.3. Distributional status of the ant species

In order to ascertain whether the species potentially benefited by the drove roads are either uncommon or widespread, we checked their distribution status in the Iberian Peninsula, using the range maps available in www.hormigas.org. To take into account that these maps could be biased by several factors (geographic distribution of myrmecologists, detectability of the different species), and could underestimate the distribution range of many

Table 1
Description of the four study locations. T: mean annual temperature; P: mean annual precipitation.

Landscape unit	Municipality (Drove road name)	Altitude (m)	Lithology & Soils	T & P	Predominant matrix
Cropland	Quijorna (Cañada Real Segoviana)	600	Arkose *Luvisols, Cambisols*	14.5 °C *500 mm*	Extensive croplands used for rainfed agriculture (mainly cereals), with scattered Holm oaks (*Quercus ilex* L.) and occasional hedgerows
Rangeland	San Agustín de Guadalix (Vereda de las Tapias de Viñuelas)	850	Granite, Gneis *Cambisols, Leptosols*	13.0 °C *600 mm*	Grasslands with scattered Holm oaks (*Q. ilex* L.) and junipers (*Juniperus oxycedrus* L.) used for extensive grazing.
Submediterranean forest	Miraflores de la Sierra (Cordel del Puerto de la Morcuera)	1250	Granite, Gneis *Cambisols Leptosols*	11 °C *650–1500 mm*	Semi-deciduous forests of *Quercus pyrenaica* L., used for occasional grazing.
Coniferous forest	San Lorenzo de El Escorial (Cañada Real Leonesa)	1450	Granite, Gneis *Leptosols, Regosols*	6–9 °C *800-1500 mm*	Forests dominated by *Pinus sylvestris* L., used for logging and occasional grazing.

species, we have considered that those species present in more than 25% of the Iberian $1° \times 1°$ cells are widespread species. The rest of species were considered uncommon.

2.4. Functional traits and functional diversity

The ideal index of functional diversity should be based on functional traits that correlate well with ecosystem function (Cadotte et al., 2011). Unfortunately, there is still little consensus about which and how many traits should be considered for this purpose (see, for example, differences between Bihn et al., 2010; Silva and Brandao, 2010). For this study, we gathered three complementary sets of variables largely related to ecosystem functioning (Table 2). First, we classified ants into functional groups following Roig and Espadaler (2010). This classification is an adaptation for the Iberian Peninsula of the previous proposals by in Andersen (1995) and Brown (2000), and is based on the value of ant species as bioindicators of ecosystem disturbance/stress. Second, the trophic niche of each species was described using five non-exclusive feeding categories. Third, five biometric variables related to food provisioning and species interactions were measured in specimens collected in the study area (averages of 10 individuals in all but the rarest species).

Functional diversity was then measured with the FDis index, the mean distance in a multidimensional trait space of individual species from the centroid of all species in an assemblage (LaLiberté and Legendre, 2010). FDis permits quantitative (e.g., our biometric variables) and qualitative descriptors of species (e.g., our functional groups and trophic niche variables). Multivariate distances

Table 2
Functional traits used to obtain the functional diversity index FDis, and weights assigned to each variable. FDis was calculated as the mean distance in a multidimensional trait space of individual species from the centroid of all species in an assemblage. The variables were weighted to place all three sets (functional groups, biometrics and trophic niche descriptors) on an equal footing.

Set of variables	Type	Variables	Weight in FDis	
Functional group	Categorical	Cryptic	1/12	1/3
		Cold climate & shade specialists	1/12	
		Generalists & opportunists	1/12	
		Hot climate & open habitat specialists	1/12	
Trophic niche	Categorical (non-exclusive)	Seeds	1/12	1/3
		Nectar	1/12	
		Animal remains	1/12	
		Aphids	1/12	
Biometry	Continuous	Eye length	1/15	1/3
		Femur length	1/15	
		Tibia length	1/15	
		Head length	1/15	
		Head width	1/15	

between samples were estimated with the Gower dissimilarity index. The variables were weighted to place all three sets (functional groups, biometrics and trophic niche descriptors) on an equal footing (Table 2).

2.5. Data analysis

Richness and functional diversity were compared amongst habitats with a permutational test based on 2000 random iterations. To assess whether the studied locations had different species and functional compositions, we applied a permutational multivariate analysis of variance using distance matrices.

To visually detect whether drove roads are keystone structures for ants, we built species accumulation curves for each location, combining the distant matrix, the adjacent matrix and the drove road. The data points for each part of the curve were calculated as the mean species richness values with all possible sampling orders. Following Tews et al. (2004), the keystone structure characteristic was recognized if an abrupt increase in the pattern of species accumulation occurred when the curve entered a new habitat type.

To explore differences in species composition amongst habitats, the species assemblages of the sampling units were submitted to a non-metric multidimensional scaling (NMDS) based on binary Bray–Curtis dissimilarities. A two-dimensional stable NMDS solution was found using several random starts.

The R 2.12.2 program and specialized libraries and functions (vegan and FD packages) were used for all statistical analyses.

3. Results

We found 42 ant species in the four locations (Appendix A). Overall numbers showed that drove roads hosted more species than matrices in forested locations, but not in open environments (Table 3). Except for the cropland locality, drove roads contributed a higher number of uncommon species, both in absolute and relative terms. The detected ant species were assigned to five functional groups (Fig. 2, Appendix B): generalists and opportunistic species (GO), hot-climate and open-habitat species (HCSOH), cold-climate and shade-habitat species (CCSSH), social parasite (P) and cryptic (C). Open environments were dominated by GO and HCSH functional groups. In forested locations, the size of these two groups progressively increased from distant matrices to drove roads.

Average species richness per sampling unit ranged from 0.8 in the Coniferous forest distant matrix to 9.2 in the Rangeland distant matrix, with drove roads reaching 6 to 8 species, depending on the location (Fig.3; Table 4). Richness and functional diversity rose simultaneously from matrices to drove road habitats in forested locations, but did not show significant differences in open environments (Tables 4 and 5, Fig. 3). Neither species richness ($F_{3,16} = 0.56$, $p = 0.65$) nor functional diversity of assemblages on cattle roads differed between locations ($F_{3,16} = 1.18$, $p = 0.35$).

Table 3
Total number of ant species recorded in the study for each location and land use combination. The first number in parentheses refers to exclusive species considering the location, while the second refers to the exclusive species regarding the whole study. The number in square brackets refers to the number of uncommon species in the Iberian Peninsula.

Landscape unit	Land use			Total
	Drove road	Adjacent matrix	Distant matrix	
Coniferous forest	16 (9) (1) [4]	8 (1) (0) [1]	3 (2) (2) [0]	19
Submediterranean forest	18 (10) (3) [4]	6 (0) (0) [1]	6 (3) (0) [0]	21
Rangeland	13 (1) (1) [4]	15 (3) (0) [3]	18 (5) (2) [3]	21
Cropland	11 (1) (0) [1]	8 (0) (0) [1]	12 (4) (2) [0]	15
Total	30	19	18	42

Species accumulation curves showed abrupt discontinuities on reaching both the adjacent matrix and the drove road in both forest locations (Fig. 4). In contrast, the aspect of the curve in the range-land location scarcely differed with changes in habitat type. In the cropland location, a short-lived increment in the accumulation pattern was noted when the adjacent matrix was reached, followed by a heavy attenuation of the accumulation pattern for the rest of this habitat type and the drove road.

The two-dimensional ordination (NMDS) of samples proved to be a suitable summary of the original Bray–Curtis dissimilarities (non-metric $R^2 = 0.95$), suggesting that forest locations on the one hand, and cropland and rangeland on the other, contained distinct ant assemblages (Fig. 5). Similarly, 35.7% of the variation in the distance matrix based on species composition could be attributed to the locations ($F_{3,48} = 8.88$, $p = 0.001$). Within the cattle road habitat, this percentage increased to 55.6% ($F_{3,16} = 6.69$, $p = 0.001$).

4. Discussion

Effects of drove roads on ant communities were heavily location-dependent, probably due to the characteristics of the surrounding matrix: drove roads increased ant biodiversity in landscapes dominated by forests, but exerted little or even a negative effect in open environments.

The positive impact of drove roads on ant species richness observed in forest locations may be a consequence of two main effects. Firstly, the presence of an active drove road in a forest environment implies the incorporation of an additional and distinct habitat type, and hence increases habitat heterogeneity The new habitat shows a savannah like structure, highly differentiated from the forest matrix, and therefore favours the occurrence open
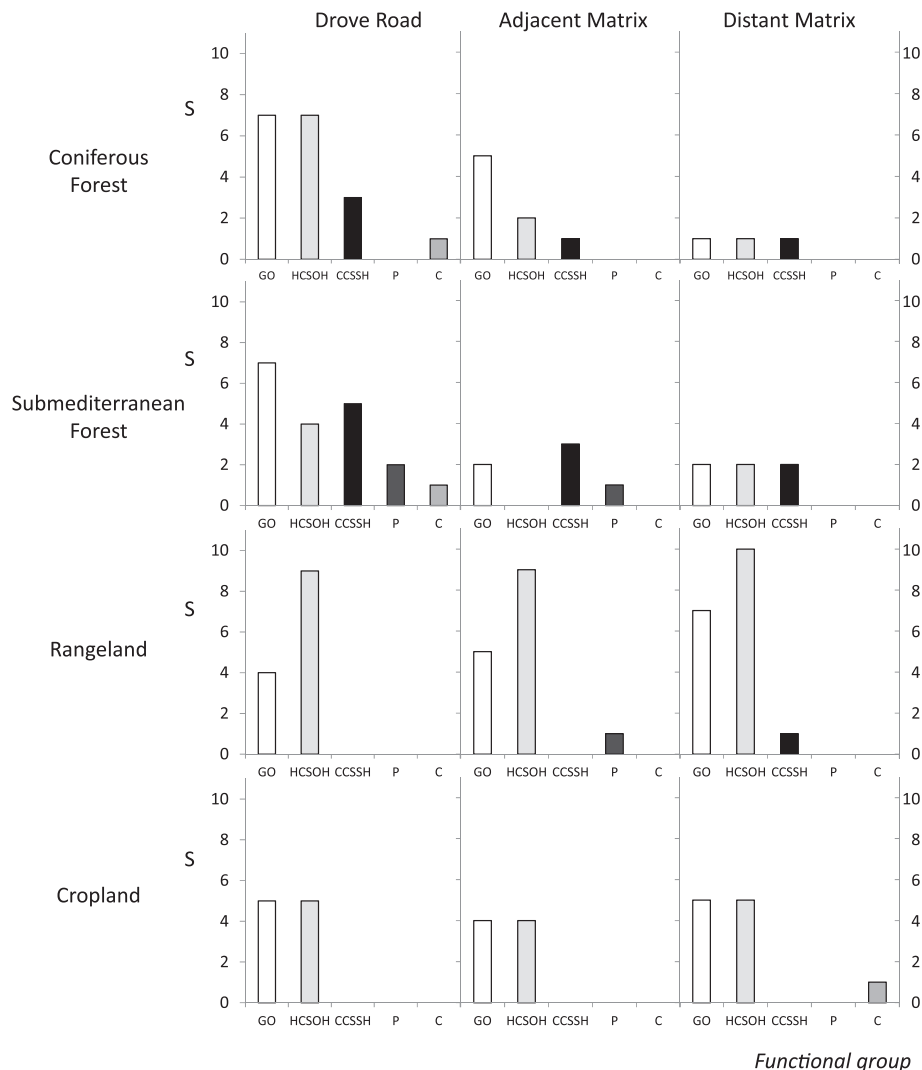
Fig. 2. Number of species (S) belonging to the different ant functional groups detected in the three habitat types and four study locations. GO, generalists and opportunistic species; HCSOH: hot-climate and open-habitat species; CCSSH: cold-climate and shade-habitat species; P: social parasite; C: cryptic.
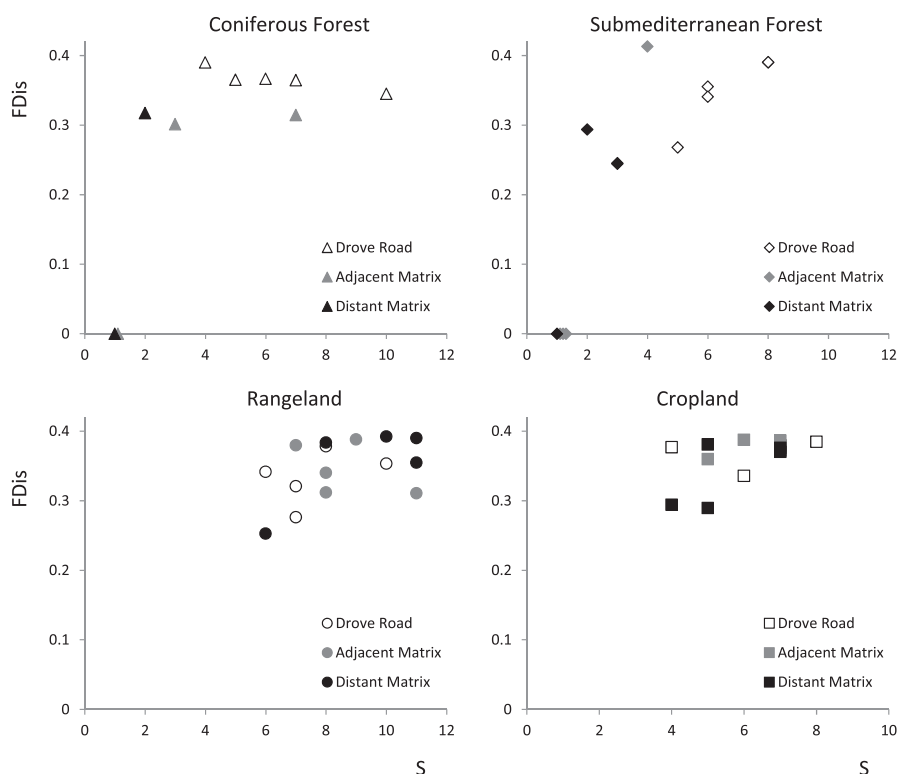
Fig. 3. Relationship between species richness (S) (*x*-axis) and functional diversity (FDis) (*y*-axis) in the four studied locations. Data have been jittered to improve representation of overlapping points.

habitat species. Indeed, while species found in the distant matrix in both the coniferous and the submediterranean forests were equally distributed in the three main functional groups, the correspondent observations in the drove roads showed a clear increase in the two functional groups more linked to open environments (hot-climate and open-habitat species; generalists and opportunists).

Secondly, species density (per sampling unit) was much higher on drove roads than in forest matrices, suggesting that the former are particularly favourable habitats for ants. To a large extent, this effect can be explained by the fact that ants are a thermophilic group (Kaspari et al., 2000), and hence most species find their resources and nesting sites in open environments (such as drove roads). Open Mediterranean grasslands are dominated by annual species producing large seed banks (Ortega et al., 1997), and not surprisingly both strict (e.g. *Messor capitatus*) and facultative (e.g. *Aphaenogaster iberica*) granivores (Azcarate and Peco, 2012) were found in drove roads but not in forests. In the same sense, scavengers *Cataglyphis rosenhauri* and *Cataglyphis iberica*, were also absent from forests but did occur in drove roads, where it is expected a higher density of arthropod corpses and is more feasible the use of the sky for reading compass information (Fourcassie et al., 2000) than under the forest canopy. Moreover, nesting possibilities are probably higher in drove roads for most species, since open environments facilitate thermoregulation (Jones and Oldroyd,

2007). Finally, the fact that drove roads are more heterogeneous than matrices (Azcárate et al., 2012) implies that they offer a wider range of both resources and nesting microhabitats to ants.

If drove roads crossing forest environments provide resources or nesting sites to ants as a species group, then they are good candidates to be considered as keystone structures (Tews et al., 2004). This condition is supported by at least two additional facts. Firstly, drove roads are distinct spatial structures within larger and more homogeneous matrices (Azcárate et al., 2012), what coincides with the physical appearance described by Tews et al. (2004) for keystone structures. Secondly, our results showed abrupt discontinuities in the species–accumulation curves when sampling transects enter drove roads, which is one of the criteria proposed by Tews et al. (2004) for the detection of keystone structures. No exotic or invasive ants were detected in drove roads crossing forest environments and, interestingly, the increase in species density in drove roads was not caused by a higher occurrence of widespread species: our data showed that not only in absolute numbers, but also in their relative frequencies, the presence of uncommon species was higher in drove roads when compared with forest matrices. This fact makes our result more significant in terms of biodiversity conservation.

Higher species richness on the drove roads in the two forests was accompanied by an increase in functional diversity. This result

Table 4
Average species richness and standard deviation per habitat in the four case study areas. Different subscripts show significant differences ($p < 0.05$) between habitats estimated by a permutational test.

	Drove road	Adjacent matrix	Distant matrix
Coniferous forest	6.4 (2.3) [a]	2.2 (2.9) [b]	0.8 (0.8) [b]
Submediterranean forest	6.6 (1.3) [a]	1.4 (1.5) [b]	1.8 (1.3) [b]
Rangeland	7.6 (1.5) [a]	8.6 (1.5) [a]	9.2 (2.2) [a]
Cropland	6.4 (1.5) [a]	6.2 (0.8) [a]	5.6 (1.3) [a]

Table 5
Average FDis and standard deviation per habitat in the four case study areas. Different subscripts show significant differences ($p < 0.05$) between habitats estimated by a permutational test.

	Drove road	Adjacent matrix	Distant matrix
Coniferous forest	1.79 (0.23) [a]	1.09 (0.95) [b]	0.51 (0.88) [b]
Submediterranean forest	1.82 (0.28) [a]	0.65 (1.30) [b]	0.69 (0.61) [b]
Rangeland	2.10 (0.26) [a]	1.95 (0.17) [a]	2.11 (0.30) [a]
Cropland	2.11 (0.23) [a]	2.29 (0.16) [a]	2.03 (0.33) [a]
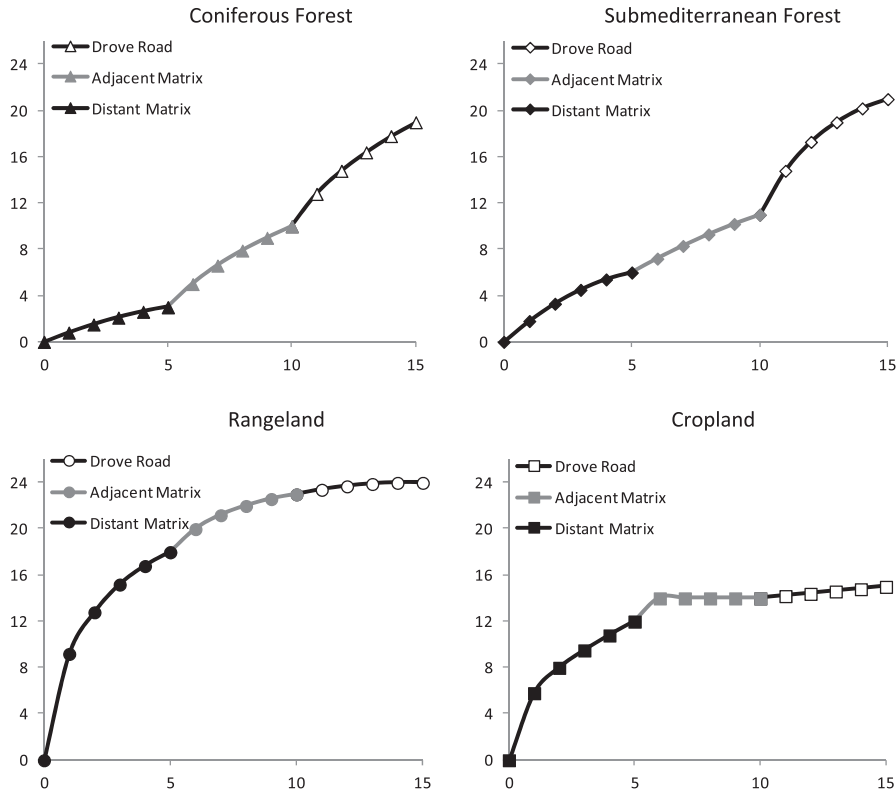
Fig. 4. Species accumulation curves of the four study locations, constructed by combining the accumulation due to the three different habitat types. Data points for each part of the curve show mean species richness (*y*-axis) for a certain number of sampling units (*x*-axis) with all possible sampling orders.

concurs with those of Bihn et al. (2010) for leaf litter ants along a successional gradient of secondary forests. It shows that the increase in richness is not at the expense of functionally redundant species. This result is compatible with the sampling effect hypothesis (SEH) (Tilman et al., 1997), which predicts that successive additive random draws from a regional species pool lead to an increase in trait states. Interestingly, ant assemblages respond to drove roads in a different way from plant assemblages, which basically increase their richness by adding functionally redundant species (Azcárate et al., 2012). An increase in ant functional diversity probably implies an increase in the number of ecological functions performed by the ant assemblage. Ants can stockpile a considerable part of primary and secondary production, develop

Fig. 5. Nonmetric multidimensional scaling of ant assemblages, according to differences (binary Bray–Curtis) in species composition.

interactions with aphids and lycaenids, host a number of invertebrates, fungi and microorganisms in their nests, and act as keystone species and ecosystem engineers (see reviews in Folgarait, 1998; MacMahon et al., 2000; Crist, 2009). In the particular case of Mediterranean systems, ants play an important role as seed predators (Azcarate and Peco, 2003, 2006; Ordonez and Retana, 2004), seed dispersers (Wolff and Debussche, 1999; Arnan et al., 2010), and also in changing the chemical and physical properties of the soil (Azcarate and Peco, 2007; Cerda and Jurgensen, 2008). We may thus deduce that drove roads crossing forested matrices are not only key structures for ant biodiversity, but also imply an increase in the number of ecological functions.

The rate of accumulation of new species shown by the species accumulation curves in forest locations not only increased on drove roads, but also in the adjacent matrix. With a few exceptions, border assemblages do not have unique species, and their species compositions are closer to those on drove roads than in distant matrices. We surmise that ant assemblages in adjacent matrices are affected by edge effects, although on the basis of our data we cannot rule which specific mechanisms are involved (Ries et al., 2004). Ants vary greatly in their responses to borders (Dauber and Wolters, 2004; Steiner and Schlick-Steiner, 2004; Sobrinho and Schoereder, 2007), and hence more detailed information would be needed for a correct interpretation of our data.

Unlike the results from forest locations, drove roads contributed little to the ant communities in the cropland and rangeland locations. In both cases, the drove road and the adjacent matrix showed no differences in species richness or functional diversity. The species accumulation curves rose slightly near the adjacent matrix, but growth slowed sharply, especially in the cropland location. The aspect of the curves does not suggest increases in richness at the location scale on the sole basis of the inclusion of a

drove road. The composition of the drove road communities also showed no substantial differences from the cropland and rangeland matrices. It is important to note that although the study location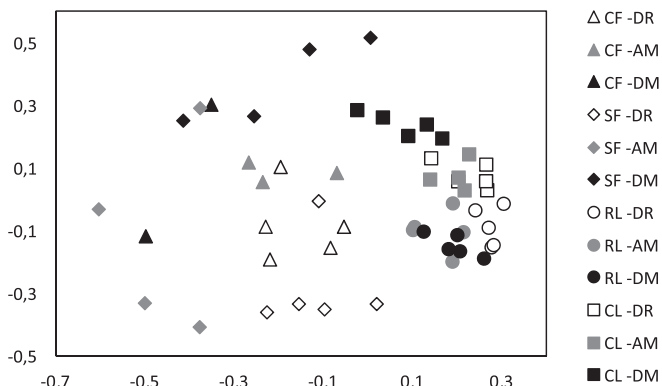s are still managed extensively, they are increasingly being replaced by more common intensive schemes, and also that ants are sensitive to agricultural and grazing intensification (Wilson et al., 1999; Philpott and Armbrecht, 2006). Thus, drove roads within these intensively managed open landscapes may indeed have higher richness values.

In summary, our study shows that active drove roads which cross forest environments act as keystone structures for ants, significantly increasing their biodiversity at both the location and the fine scale. This effect is seen in terms of both species and functional diversity, and probably has a strong impact on ecosystem functioning. Drove road effects could be shared with other types of gaps occurring in the forest landscapes not considered in this study. However, Mediterranean areas are undergoing a sustained loss of mosaic landscapes (including both woody and open habitats) in favour of larger homogeneous forest land cover (Debussche et al., 1999). In this context, the conservation of well-preserved drove roads can be seen as a good opportunity to keep a minimum level of spatial heterogeneity in forest landscapes. Although the present study did not detect relevant effects in extensive grasslands or croplands, a major role played by drove roads in intensified agroecosystems must not be ruled out. Our findings thus corroborate that drove roads play a relevant ecological role in Mediterranean ecosystems, and support the claim that transhumance and the drove road network should be protected due to their positive effects on biodiversity, ecosystem functioning and the production of ecosystem services.

Acknowledgements

Appendix A. Distributional status and occurrence of the sampled species in the four locations and habitat types. Species present in less than 25% of the 1° by 1° cells of the distribution maps available un www.hormigas.org were considered as "Uncommon species". One species could not be identified ("Unknown"), and two other species could not be identified at the species level (labelled *Myrmica* A and B).

Species	Coniferous forest			Submediterranean forest			Rangeland			Cropland			Uncommon species
	DR	AM	DM	DR	AM	DM	DR	AM	DM	DR	AM	DM	
Aphaenogaster dulcineae												x	x
Aphaenogaster iberica	x			x			x	x	x				
Aphaenogaster senilis		x					x	x		x	x	x	
Camponotus aethiops						x	x	x	x	x	x	x	
Camponotus cruentatus							x	x	x	x	x	x	
Camponotus foreli	x					x							
Camponotus micans			x										
Camponotus piceus	x			x									
Camponotus pilicornis							x	x	x			x	
Camponotus sylvaticus							x						
Cataglyphis iberica	x							x		x			
Cataglyphis rosenhauri	x	x		x			x	x	x	x	x		x
Crematogaster auberti	x	x					x		x	x		x	
Crematogaster scutellaris	x	x	x	x	x	x		x	x	x	x	x	
Formica cunicularia	x	x							x				
Formica dusmeti	x			x									x
Formica fusca	x	x						x	x				
Formica polyctena	x			x									x
Formica pratensis				x	x								
Formica rufa					x								x
Formica rufibarbis				x									
Formica sanguinea				x	x								
Formica subrufa				x				x					
Goniomma blanci				x									x
Goniomma hispanica								x					
Lasius alienius								x					
Lasius brunneus			x										
Lasius flavus	x			x									
Lasius grandis				x		x							
Lasius niger	x	x				x							
Messor barbarus							x	x	x	x	x	x	
Messor bouvieri									x			x	
Messor capitatus	x												
Messor hispanicus							x	x					x
Myrmica A				x									
Myrmica B				x	x			x					
Oxyopomyrmex saulcyi							x		x				x
Pheidole pallidula				x			x		x	x	x	x	
Proformica ferreri	x						x	x	x				x
Tapinoma erraticum	x			x	x				x				
Tapinoma nigerrimum	x			x		x	x	x	x	x	x	x	
Tetramorium caespitum	x	x		x									
Unknown												x	

Appendix B. Sampled species in all four locations and three sets of variables used to estimate functional diversity. Functional group as per Roig and Espadaler (2010): GO, generalists and opportunistic species; HCSOH: hot-climate and open-habitat species; CCSSH: cold-climate and shade-habitat species; P: social parasite; C: cryptic. Variables describing the trophic niche indicate whether the species uses different types of resources: aphids, for farm aphids; predator for active predation on invertebrates; grain and nectar for taking respectively seeds and nectar, and animal remains for scavenging. Biometry shows averages for our own measurements (all data in mm). Two species could not be identified at the species level (labelled *Myrmica* A and B) and trophic niche was imputed according to what is known about the genera.

Species	Functional group	Trophic niche					Biometry				
		Aphids	Predator	Grain	Nectar	Animal remains	Head length	Head width	Tibia length	Femur length	Eye length
Aphaenogaster dulcineae	C	0	1	1	0	1	0.57	1.02	1.08	1.44	0.25
Aphaenogaster iberica	GO	0	1	1	0	1	1.31	1.03	1.93	2.54	0.24
Aphaenogaster senilis	GO	0	1	1	0	1	1.75	1.16	1.91	2.61	0.27
Camponotus aethiops	HCSOH	1	1	0	0	0	2.17	1.11	1.91	2.04	0.36
Camponotus cruentatus	HCSOH	1	1	0	0	0	2.32	1.61	2.86	3.04	0.47
Camponotus foreli	HCSOH	1	1	0	0	0	1.62	1.07	1.46	1.50	0.18
Camponotus micans	HCSOH	1	1	0	0	0	1.95	1.19	1.89	1.99	0.30
Camponotus piceus	HCSOH	1	1	0	0	0	1.12	0.89	0.82	0.77	0.00
Camponotus pilicornis	HCSOH	1	1	0	0	0	2.50	1.25	2.37	2.56	0.48
Camponotus sylvaticus	HCSOH	1	1	0	0	0	2.21	1.28	2.23	2.37	0.39
Cataglyphis iberica	HCSOH	0	0	0	0	1	1.52	1.44	2.20	2.49	0.47
Cataglyphis rosenhauri	HCSOH	0	0	0	0	1	1.48	1.39	2.17	2.46	0.46
Crematogaster auberti	GO	1	0	0	0	0	1.00	0.94	0.74	0.93	0.24
Crematogaster scutellaris	GO	1	0	0	0	0	1.01	0.97	0.76	0.96	0.26
F. cunicularia	HCSOH	1	1	0	0	0	1.48	1.18	1.63	1.83	0.47
F. dusmeti	CCSSH	1	1	0	0	0	1.63	1.04	1.46	1.67	0.44
F. fusca	GO	1	1	0	0	0	1.42	1.15	1.55	1.72	0.47
F. polyctena	CCSSH	1	1	0	0	0	1.85	1.04	1.53	1.72	0.45
F. pratensis	CCSSH	1	1	0	0	0	1.85	1.84	2.44	2.66	0.55
F. rufa	CCSSH	1	1	0	0	0	1.69	1.89	2.37	2.59	0.54
F. rufibarbis	GO	1	1	0	0	0	1.51	1.15	1.59	1.78	0.46
F. sanguinea	CCSSH	1	1	0	0	0	1.73	1.36	1.90	2.09	0.52
F. subrufa	HCSOH	1	1	0	0	0	1.50	1.04	1.55	1.76	0.45
Goniomma blanci	HCSOH	0	0	1	0	0	0.85	0.98	0.81	1.20	0.30
Goniomma hispanica	HCSOH	0	0	1	0	0	0.81	0.91	0.62	0.88	0.28
Lasius alienius	CCSSH	1	1	0	0	0	0.85	0.84	0.62	0.81	0.22
Lasius brunneus	CCSSH	1	1	0	0	0	0.95	0.77	0.81	0.90	0.21
Lasius flavus	C	1	1	0	0	0	0.90	0.92	0.74	0.83	0.14
Lasius grandis	CCSSH	1	1	0	0	0	1.04	1.04	1.14	1.26	0.28
Lasius niger	CCSSH	1	1	0	0	0	0.98	0.93	0.96	1.07	0.23
Messor barbarus	HCSOH	0	0	1	0	0	2.04	1.51	1.42	1.68	0.30
Messor bouvieri	HCSOH	0	0	1	0	0	1.50	1.36	1.10	1.65	0.30
Messor capitatus	HCSOH	0	0	1	0	0	1.83	1.74	1.62	2.12	0.36
Messor hispanicus	HCSOH	0	0	1	0	0	1.14	1.31	1.39	1.85	0.29
Myrmica A	P	0	1	0	1	1	1.17	1.05	0.80	1.14	0.24
Myrmica B	P	0	1	0	1	1	1.16	0.95	0.81	1.16	0.25
O. saulcyi	HCSOH	0	0	1	0	0	0.59	0.60	0.45	0.64	0.19
Pheidole pallidula	GO	0	1	0	1	1	0.96	0.55	0.51	0.72	0.14
Proformica ferreri	HCSOH	0	1	0	1	1	0.83	0.58	0.89	0.96	0.24
Tapinoma erraticum	GO	1	0	0	0	1	0.65	0.50	0.56	0.68	0.17
Tapinoma nigerrimum	GO	1	0	0	0	1	0.95	0.75	0.73	0.81	0.21
Tetramorium caespitum	GO	0	0	1	0	0	0.80	0.75	0.42	0.72	0.15

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