

Drove roads: keystone structures that promote ant diversity in

Mediterranean forest landscapes

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Abstract

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.

Keywords: Transhumance; Functional diversity; Spatial heterogeneity; Grasslands; Ant assemblages

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 125,000km (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 epizoochorous 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 (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; Azcárate and Peco, 2011). 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 300m-400m long by 40-50m wide. Three habitat 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 75m, while the distant matrix was more than 200m 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 x 5 cm deep) forming a triangle with vertexes one metre apart (for ground-dwelling species) and (2) a set of three baits in different trees less than 10 metres 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 1cm³ of honey and 1 cm³ of tuna in oil, was placed at a height of 1.5m on the tree trunk, then checked after 30 minutes. We recorded all ant species detected within 1 metre of the bait in a 2-minute 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 species, we have considered that those species present in more than 25% of the Iberian 1°x1° 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 and Silva et al., 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 Espalader (2010). This classification is an adaptation for the Iberian Peninsula of the previous proposals by 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 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 (Table 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 ($F_{3,16} = 1.18$, $p = 0.35$).

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 rangeland 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

263 increased ant biodiversity in landscapes dominated by forests, but exerted little
 264 or even a negative effect in open environments.
 265
 266 The positive impact of drove roads on ant species richness observed in forest
 267 locations may be a consequence of two main effects. Firstly, the presence of an
 268 active drove road in a forest environment implies the incorporation of an
 269 additional and distinct habitat type, and hence increases habitat heterogeneity
 270 The new habitat shows a savannah like structure, highly differentiated from the
 271 forest matrix, and therefore favours the occurrence open habitat species.
 272 Indeed, while species found in the distant matrix in both the coniferous and the
 273 submediterranean forests were equally distributed in the three main functional
 274 groups, the correspondent observations in the drove roads showed a clear
 275 increase in the two functional groups more linked to open environments (hot-
 276 climate and open-habitat species; generalists and opportunists).
 277
 278 Secondly, species density (per sampling unit) was much higher on drove roads
 279 than in forest matrices, suggesting that the former are particularly favourable
 280 habitats for ants. To a large extent, this effect can be explained by the fact that
 281 ants are a thermophilic group (Kaspari et al. 2000), and hence most species
 282 find their resources and nesting sites in open environments (such as drove
 283 roads). Open Mediterranean grasslands are dominated by annual species
 284 producing large seed banks (Ortega et al. 2003), and not surprisingly both strict
 285 (e.g. *Messor capitatus*) and facultative (e.g. *Aphaenogaster iberica*) granivores
 286 (Azcárate and Peco 2012) were found in drove roads but not in forests. In the
 287 same sense, scavengers *Cataglyphis rosenhauri* and *C. 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.

313

314 Higher species richness on the drove roads in the two forests was accompanied
315 by an increase in functional diversity. This result concurs with those of Bihn et
316 al. (2010) for leaf litter ants along a successional gradient of secondary forests.
317 It shows that the increase in richness is not at the expense of functionally
318 redundant species. This result is compatible with the sampling effect hypothesis
319 (SEH) (Tilman et al. 1997), which predicts that successive additive random
320 draws from a regional species pool lead to an increase in trait states.
321 Interestingly, ant assemblages respond to drove roads in a different way from
322 plant assemblages, which basically increase their richness by adding
323 functionally redundant species (Azcárate et al., 2012). An increase in ant
324 functional diversity probably implies an increase in the number of ecological
325 functions performed by the ant assemblage. Ants can stockpile a considerable
326 part of primary and secondary production, develop interactions with aphids and
327 lycaenids, host a number of invertebrates, fungi and microorganisms in their
328 nests, and act as keystone species and ecosystem engineers (see reviews in
329 Folgarait, 1998; MacMahon et al., 2000 and Crist, 2009). In the particular case
330 of Mediterranean systems, ants play an important role as seed predators
331 (Azcárate and Peco, 2003, 2006; Ordóñez and Retana, 2004), seed dispersers
332 (Wolff and Debussche, 1999; Arnan et al., 2010), and also in changing the
333 chemical and physical properties of the soil (Azcárate et al., 2007; Cerdá and
334 Jurgensen, 2008). We may thus deduce that drove roads crossing forested
335 matrices are not only key structures for ant biodiversity, but also imply an
336 increase in the number of ecological functions.

337

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 Schroeder, 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 locations 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; Andersen et al., 2002; Philpott and Armbrrecht, 2006). Thus, drove roads within these intensively managed open landscapes may indeed have higher richness values.

363

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

382

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384

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540 Agriculture Ecosystems & Environment 75, 13-30.
541 Wolff, A., Debussche, M., 1999. Ants as seed dispersers in a Mediterranean old-
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543

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

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

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
		Cold Climate & Shade Specialists	1/12
		Generalists & Opportunists	1/12
		Hot Climate & Open Habitat Specialists	1/12
			1/3
Trophic Niche	Categorical (non-exclusive)	Seeds	1/12
		Nectar	1/12
		Animal remains	1/12
		Aphids	1/12
Biometry	Continuous	Eye length	1/15
		Femur length	1/15
		Tibia length	1/15
		Head length	1/15
		Head width	1/15
			1/3

553 Table 3. Total number of ant species recorded in the study for each location and
 554 land use combination. The first number in parentheses refers to exclusive
 555 species considering the location, while the second refers to the exclusive
 556 species regarding the whole study. The number in square brackets refers to the
 557 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

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559

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

	Drove	Adjacent	Distant
	road	matrix	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

562 Table 5. Average FDis and standard deviation per habitat in the four case study
 563 areas. Different subscripts show significant differences ($p < 0.05$) between
 564 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

Figures

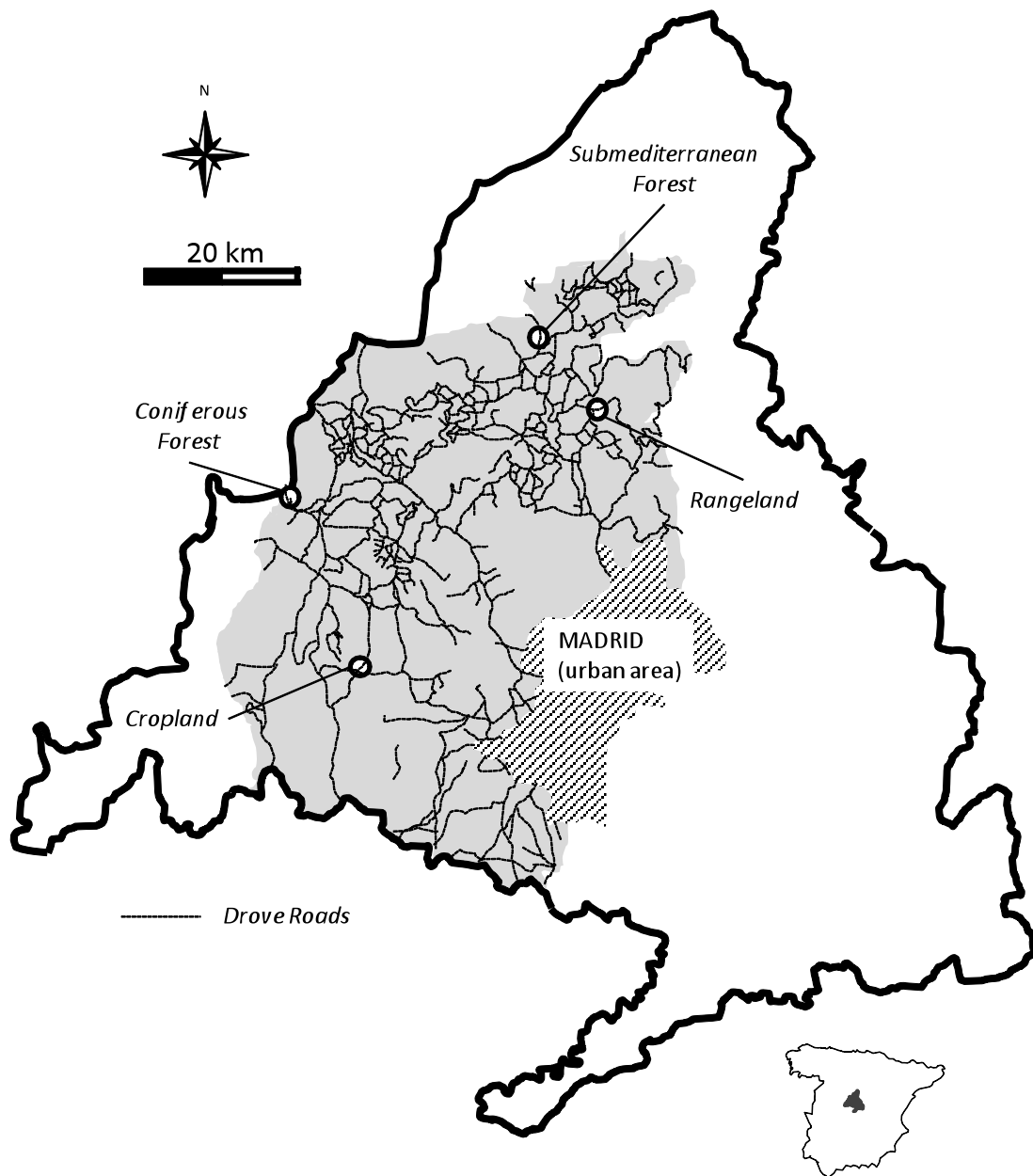
Figure 1. Study area in the Madrid Autonomous Region (Spain). The map shows the study locations and the drove road network. The drove road distribution is taken from the official map in www.madrid.org.

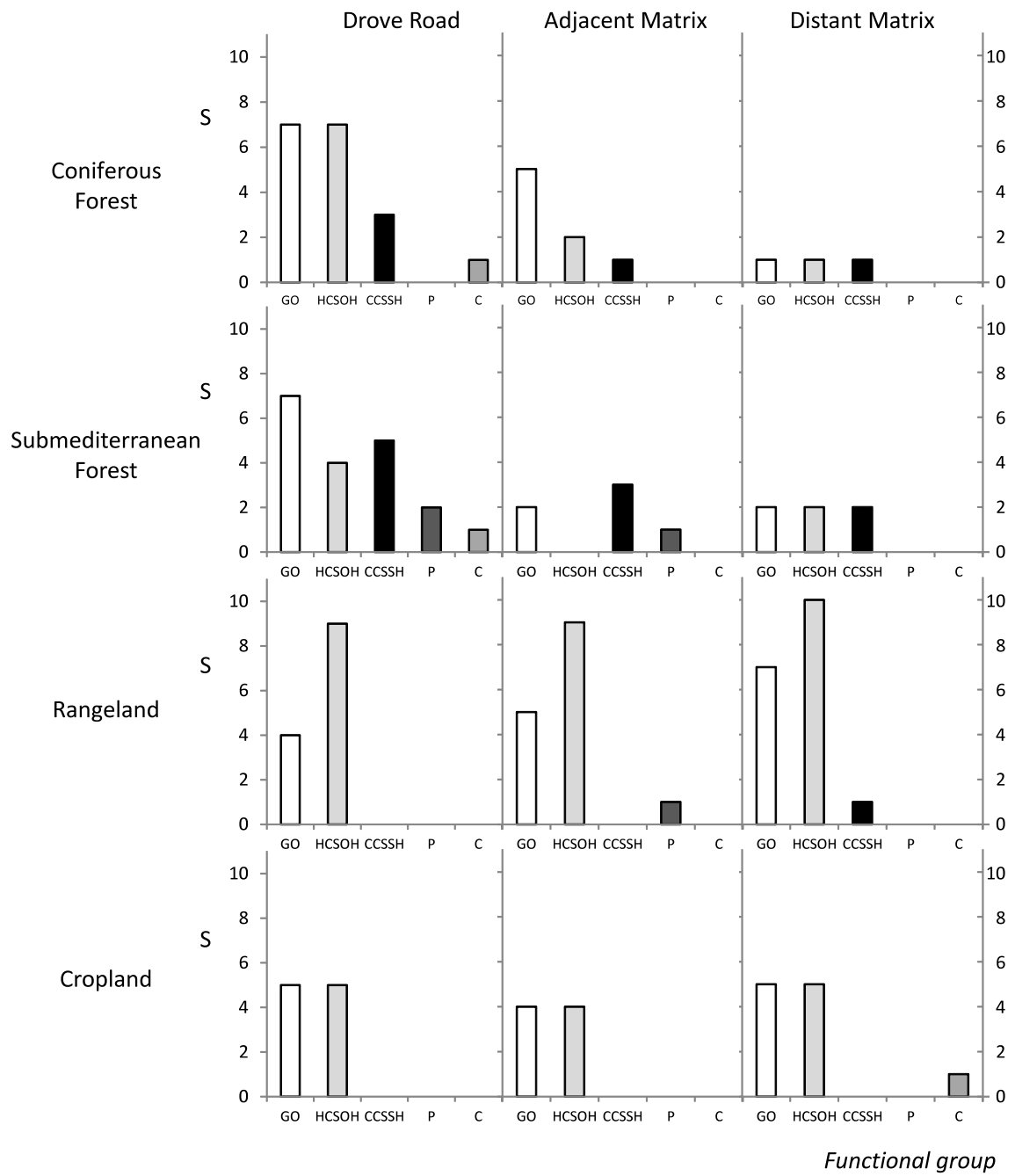
Figure 2. Number of species (S) belonging to the different ant functional groups detected in the three habitat types and four study locations. GO, generalists and opportunistic species; HCSOH: hot-climate and open-habitat species; CCSSH: cold-climate and shade-habitat species; P: social parasite; C: cryptic

Figure 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.

Figure 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.

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





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592 Figure 2.

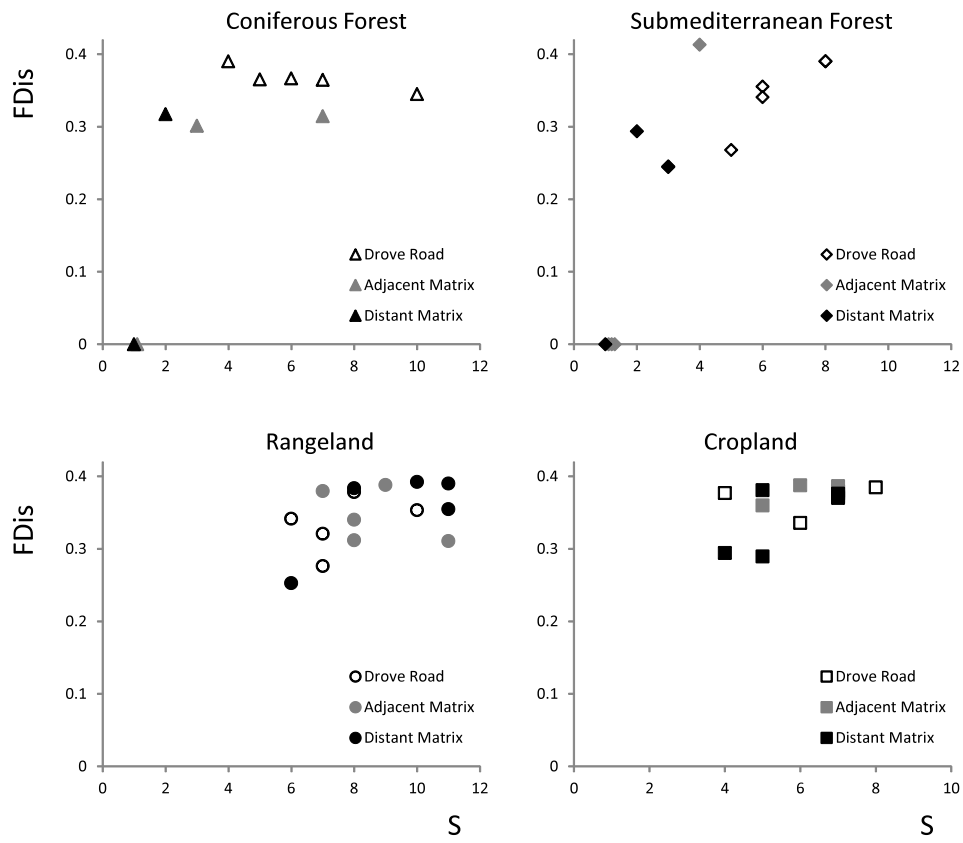
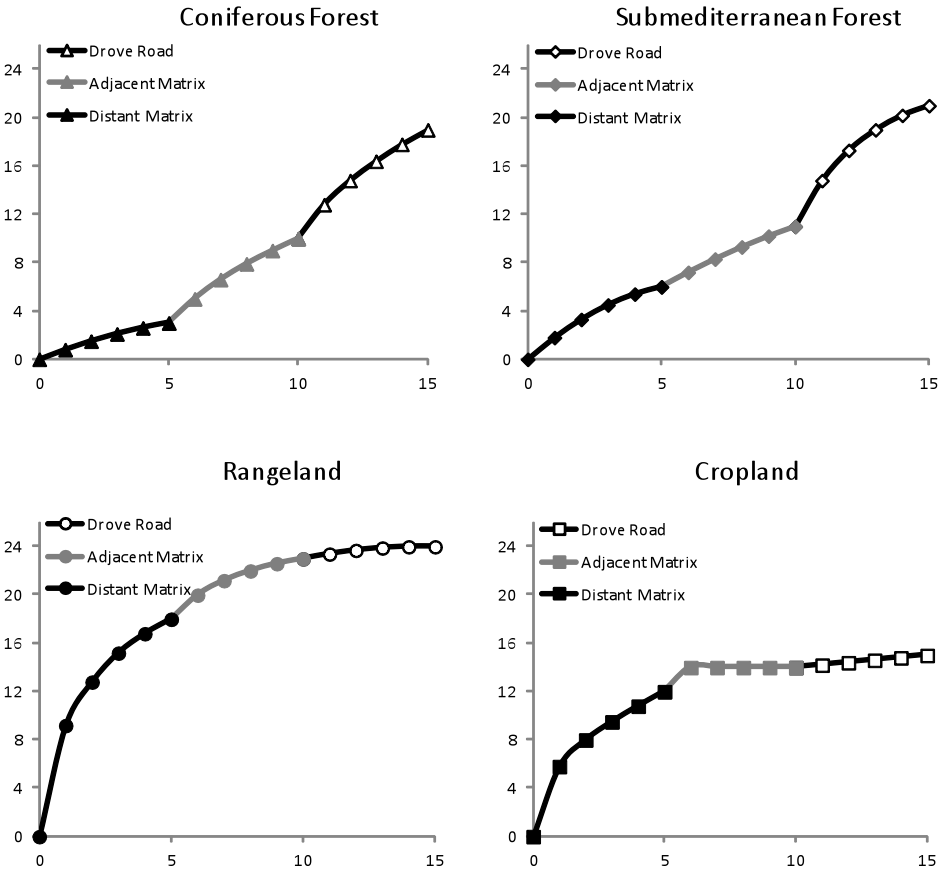


Figure 3.

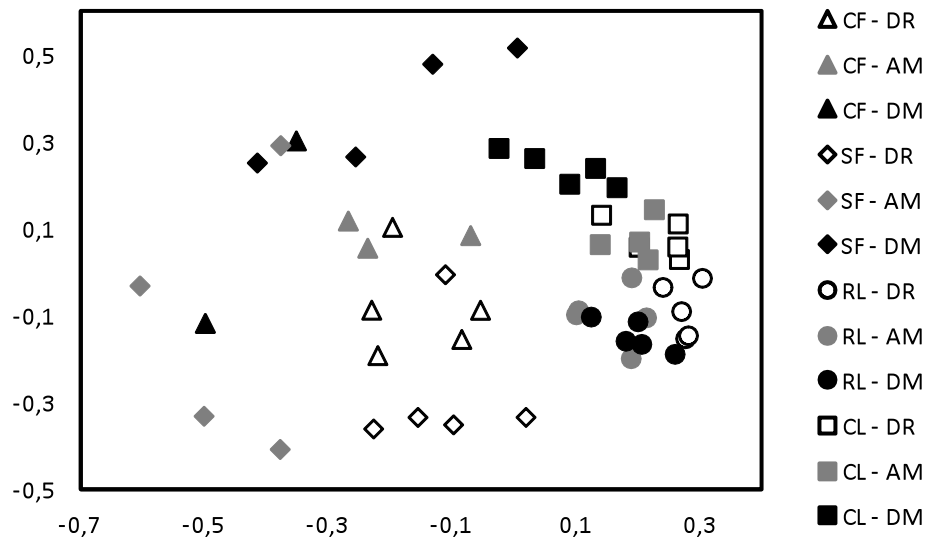
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598 Figure 4.

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601 Figure 5.

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