1 **Drove roads: keystone structures that promote ant diversity in**

2 **Mediterranean forest landscapes**

3

4

5 Francisco M. Azcárate[a,*], Javier Seoane[a], Sara Castro[b], Begoña Peco[a]

6

7 [a]TEG, Departamento de Ecología, Universidad Autónoma de Madrid. 28049,

8 Spain

9 [b]Unidad de Zoología, Departamento de Biología, Universidad Autónoma de

10 Madrid. 28049, Spain

11

12 [*] Corresponding author: Tel.: +34 91 497 3513; fax: +34 91 497 8001. E-mail

13 address: fm.azcarate@uam.es

14

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.

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.

63 The few published ecological studies of drove roads have focused on their

64 effects on plant communities. Drove roads have traditionally been regarded as a

65 good example of ecological corridors for plant species (review in Bunce et al.,

66 2006), although no experimental evidence supported this view until Manzano

67 and Malo (2006) detected epizoochorous seed dispersal over distances of up to

68 400 km. More recently, the effects of drove roads on landscape patterns,

69 species composition and functional diversity of plant communities have been

70 measured (Azcárate et al, 2012), showing that drove roads are a source of

71 spatial heterogeneity and a reservoir for many plant species in non- or

72 moderately-grazed habitats.

73

74 Drove roads could also have a noticeable effect on the diversity and

75 composition of animal assemblages. Active drove roads maintain patches of

76 open grassland in non-grazed environments such as forests, and hence

77 increase spatial heterogeneity. Spatial heterogeneity and diversity of several

78 animal species groups are often (but not always) correlated (Duelli, 1997; Atauri

79 and de Lucio, 2001; Szczepko et al., 2012). It has been argued that each

80 animal species group depends on a specific structural aspect of the vegetation

81 whose presence or quality can be detected at a certain spatial scale (Tews et

82 al, 2004). At that scale, biodiversity is favoured by the occurrence of "keystone

83 structures", characterized by their ability to provide resources, shelter or nesting

84 sites to that species group. Examples of keystone structures at different spatial

85 scales are tree cavities in forests (for insects, birds and mammals), trees in

86 African savannas (for arboreal rodents, ungulates, raptors and other species

87 groups) and temporary wetlands in agricultural fields (for carabid beetles) (Tews

4

88   et al., 2004; Remm and Lohmus, 2011). If a key structure affects several

89   species groups, or groups with a strong influence on ecosystem functioning,

90   then its conservation is of crucial importance. Drove roads might then function

91   as keystone structures by favouring rich groups of terrestrial species with

92   relevant roles on ecosystem functioning, such as ants.

93

94   Ants are considered to be a focal group for the monitoring of terrestrial

95   ecosystems (Underwood and Fisher, 2006; Crist, 2009). This is not surprising,

96   given their ability to stockpile a considerable amount of primary and secondary

97   production, interact with several organisms and act as ecosystem engineers

98   (Folgarait, 1998; MacMahon et al., 2000; Crist, 2009). Literature shows that

99   ants respond strongly to land management (Bestelmeyer and Wiens, 1996;

100   Chen et al., 2011), and are sensitive to different levels of grazing (Read and

101   Andersen, 2000; Boulton et al. 2005; Azcárate and Peco, 2011). Moreover, ants

102   are widespread, moderately diverse and easy to sample (Alonso and Agosti,

103   2000; Andersen et al., 2004). Their role as indicators has improved with the

104   development of the concept of functional groups to classify ants within species

105   assemblages, as first proposed in Australia (Andersen, 1995), and then

106   extended worldwide (Brown, 2000). More recently, the role of ants in ecosystem

107   functioning has been studied by measuring their functional diversity (Bihn et al.,

108   2010; Silva and Brandao, 2010) although this approach has still been little

109   addressed, in contrast to other taxa.

110

111   The present study evaluates the role of drove roads as keystone structures.

112   Specifically, our work analyzes the effects of drove roads on ant assemblages

113   by measuring species richness, functional diversity and species composition on

114   active drove roads and in the surrounding landscape matrices. Four sites were

115   chosen in different traditional Mediterranean landscapes along a gradient of

116   forest growth. We expected the effects to be dependent on the location,

117   increasing with structural differences between the drove road and the ecological

118   matrix.

119

120   **2. Materials and Methods**

121

122   2.1.   Study area

123

124   The study was done on the siliceous southern pediment of the Guadarrama

125   Range (Madrid Autonomous Region, Central Spain, Fig. 1; Table 1). The four

126   selected locations along a forest gradient were representative of the major

127   landscape units in the area (Coniferous forest, Sub-Mediterranean forest,

128   Rangeland and Cropland). All locations included a drove road with moderate

129   grazing intensity and no sign of land disturbance by non-livestock agents. In all

130   cases, the ecological matrix was well preserved and managed in a similar way

131   to traditional land uses for at least the last 30 years.

132

133   2.2.   Sampling design

134

135   In each location, we selected an approx. 2 ha drove road fragment of about

136   300m-400m long by 40-50m wide. Three habitat types were distinguished in

137   each location: the drove road itself, the adjacent matrix and the distant matrix.

138   The adjacent matrix was located between the edge of the drove road and a

139   distance of 75m, while the distant matrix was more than 200m from the edge.

140   Both types of matrices were structurally similar, but were considered separately

141   to take into account potential edge effects in the adjacent matrix. The slope and

142   aspect of the three habitat types (drove road, adjacent matrix and distant

143   matrix) were similar in each location.

144

145   Sampling was performed in July 2010. Fifteen sampling units were randomly

146   arranged in each location, five per habitat type. All sampling units of the same

147   habitat type were included in the 2 ha area, set at least 25 m apart. One

148   sampling unit consisted of (1) a set of three pitfall traps (2 cm diameter x 5 cm

149   deep) forming a triangle with vertexes one metre apart (for ground-dwelling

150   species) and (2) a set of three baits in different trees less than 10 metres apart

151   (for arboreal species). The pitfall traps were filled with a mixture of 70% ethanol

152   and 30% mono-ethylene glycol, and left in the field for 5 days. The bait, a

153   combination of 1cm^3 of honey and 1 cm^3 of tuna in oil, was placed at a height of

154   1.5m on the tree trunk, then checked after 30 minutes. We recorded all ant

155   species detected within 1 metre of the bait in a 2-minute observation. Each

156   sampling unit was characterized by the complete list of species detected using

157   both methods.

158

159   2.3.   Distributional status of the ant species

160

161   In order to ascertain whether the species potentially benefited by the drove

162   roads are either uncommon or widespread, we checked their distribution status

163   in the Iberian Peninsula, using the range maps available in www.hormigas.org.

164   To take into account that these maps could be biased by several factors

165   (geographic distribution of myrmecologists, detectability of the different

166   species), and could underestimate the distribution range of many species, we

167   have considered that those species present in more than 25% of the Iberian

168   1º×1º cells are widespread species. The rest of species were considered

169   uncommon.

170

171   2.4.   Functional traits and functional diversity

172

173   The ideal index of functional diversity should be based on functional traits that

174   correlate well with ecosystem function (Cadotte et al., 2011). Unfortunately,

175   there is still little consensus about which and how many traits should be

176   considered for this purpose (see, for example, differences between Bihn et al.,

177   2010 and Silva et al., 2010). For this study, we gathered three complementary

178   sets of variables largely related to ecosystem functioning (Table 2). First, we

179   classified ants into functional groups following Roig and Espalader (2010). This

180   classification is an adaptation for the Iberian Peninsula of the previous

181   proposals by in Andersen (1995) and Brown (2000), and is based on the value

182   of ant species as bioindicators of ecosystem disturbance/stress. Second, the

183   trophic niche of each species was described using five non-exclusive feeding

184   categories. Third, five biometric variables related to food provisioning and

185   species interactions were measured in specimens collected in the study area

186   (averages of 10 individuals in all but the rarest species).

187

188 Functional diversity was then measured with the FDis index, the mean distance

189 in a multidimensional trait space of individual species from the centroid of all

190 species in an assemblage (LaLiberté and Legendre, 2010). FDis permits

191 quantitative (e.g., our biometric variables) and qualitative descriptors of species

192 (e.g., our functional groups and trophic niche variables). Multivariate distances

193 between samples were estimated with the Gower dissimilarity index. The

194 variables were weighted to place all three sets (functional groups, biometrics

195 and trophic niche descriptors) on an equal footing (Table 2).

196

197 2.5.   Data analysis

198

199 Richness and functional diversity were compared amongst habitats with a

200 permutational test based on 2000 random iterations. To assess whether the

201 studied locations had different species and functional compositions, we applied

202 a permutational multivariate analysis of variance using distance matrices.

203

204 To visually detect whether drove roads are keystone structures for ants, we built

205 species accumulation curves for each location, combining the distant matrix, the

206 adjacent matrix and the drove road. The data points for each part of the curve

207 were calculated as the mean species richness values with all possible sampling

208 orders. Following Tews et al. (2004), the keystone structure characteristic was

209 recognized if an abrupt increase in the pattern of species accumulation

210 occurred when the curve entered a new habitat type.

211

212 To explore differences in species composition amongst habitats, the species

213   assemblages of the sampling units were submitted to a non-metric

214   multidimensional scaling (NMDS) based on binary Bray-Curtis dissimilarities. A

215   two-dimensional stable NMDS solution was found using several random starts.

216

217   The R 2.12.2 program and specialized libraries and functions (vegan and FD

218   packages) were used for all statistical analyses.

219

220   3. **Results**

221

222   We found 42 ant species in the four locations (Appendix A). Overall numbers

223   showed that drove roads hosted more species than matrices in forested

224   locations, but not in open environments (Table 3). Except for the cropland

225   locality, drove roads contributed a higher number of uncommon species, both in

226   absolute and relative terms. The detected ant species were assigned to five

227   functional groups (Fig. 2, Appendix B): generalists and opportunistic species

228   (GO), hot-climate and open-habitat species (HCSOH), cold-climate and shade-

229   habitat species (CCSSH), social parasite (P) and cryptic (C). Open

230   environments were dominated by GO and HCSH functional groups. In forested

231   locations, the size of these two groups progressively increased from distant

232   matrices to drove roads.

233

234   Average species richness per sampling unit ranged from 0.8 in the Coniferous

235   forest distant matrix to 9.2 in the Rangeland distant matrix, with drove roads

236   reaching 6 to 8 species, depending on the location (Fig.3; Table 4). Richness

237   and functional diversity rose simultaneously from matrices to drove road

238 habitats in forested locations, but did not show significant differences in open

239 environments (Table 4 and 5, Fig. 3). Neither species richness ($F_{3,16}$ = 0.56, p =

240 0.65) nor functional diversity of assemblages on cattle roads differed between

241 locations ($F_{3,16}$ = 1.18, p = 0.35).

242

243 Species accumulation curves showed abrupt discontinuities on reaching both

244 the adjacent matrix and the drove road in both forest locations (Fig. 4). In

245 contrast, the aspect of the curve in the rangeland location scarcely differed with

246 changes in habitat type. In the cropland location, a short-lived increment in the

247 accumulation pattern was noted when the adjacent matrix was reached,

248 followed by a heavy attenuation of the accumulation pattern for the rest of this

249 habitat type and the drove road.

250

251 The two-dimensional ordination (NMDS) of samples proved to be a suitable

252 summary of the original Bray-Curtis dissimilarities (non-metric R^2 = 0.95),

253 suggesting that forest locations on the one hand, and cropland and rangeland

254 on the other, contained distinct ant assemblages (Fig. 5). Similarly, 35.7% of the

255 variation in the distance matrix based on species composition could be

256 attributed to the locations ($F_{3,48}$ = 8.88, p = 0.001). Within the cattle road habitat,

257 this percentage increased to 55.6% ($F_{3,16}$ = 6.69, p = 0.001).

258

259 4. **Discussion**

260

261 Effects of drove roads on ant communities were heavily location-dependent,

262 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

12

288 absent from forests but did occur in drove roads, where it is expected a higher

289 density of arthropod corpses and is more feasible the use of the sky for reading

290 compass information (Fourcassie et al. 2000) than under the forest canopy.

291 Moreover, nesting possibilities are probably higher in drove roads for most

292 species, since open environments facilitate thermoregulation (Jones and

293 Oldroyd 2007). Finally, the fact that drove roads are more heterogeneous than

294 matrices (Azcárate et al. 2012) implies that they offer a wider range of both

295 resources and nesting microhabitats to ants.

296

297 If drove roads crossing forest environments provide resources or nesting sites

298 to ants as a species group, then they are good candidates to be considered as

299 keystone structures (Tews et al. 2004). This condition is supported by at least

300 two additional facts. Firstly, drove roads are distinct spatial structures within

301 larger and more homogeneous matrices (Azcárate et al. 2012), what coincides

302 with the physical appearance described by Tews et al. (2004) for keystone

303 structures. Secondly, our results showed abrupt discontinuities in the species–

304 accumulation curves when sampling transects enter drove roads, which is one

305 of the criteria proposed by Tews et al. (2004) for the detection of keystone

306 structures. No exotic or invasive ants were detected in drove roads crossing

307 forest environments and, interestingly, the increase in species density in drove

308 roads was not caused by a higher occurrence of widespread species: our data

309 showed that not only in absolute numbers, but also in their relative frequencies,

310 the presence of uncommon species was higher in drove roads when compared

311 with forest matrices. This fact makes our result more significant in terms of

312 biodiversity conservation.

313

Higher species richness on the drove roads in the two forests was accompanied

by an increase in functional diversity. This result 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 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 and Crist, 2009). In the particular case

of Mediterranean systems, ants play an important role as seed predators

(Azcárate and Peco, 2003, 2006; Ordóñez 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 (Azcárate et al., 2007; Cerdá 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.

337

338   The rate of accumulation of new species shown by the species accumulation

339   curves in forest locations not only increased on drove roads, but also in the

340   adjacent matrix. With a few exceptions, border assemblages do not have

341   unique species, and their species compositions are closer to those on drove

342   roads than in distant matrices. We surmise that ant assemblages in adjacent

343   matrices are affected by edge effects, although on the basis of our data we

344   cannot rule which specific mechanisms are involved (Ries et al., 2004)..Ants

345   vary greatly in their responses to borders (Dauber and Wolters, 2004; Steiner

346   and Schlick-Steiner, 2004; Sobrinho and Schroeder, 2007), and hence more

347   detailed information would be needed for a correct interpretation of our data.

348

349   Unlike the results from forest locations, drove roads contributed little to the ant

350   communities in the cropland and rangeland locations. In both cases, the drove

351   road and the adjacent matrix showed no differences in species richness or

352   functional diversity. The species accumulation curves rose slightly near the

353   adjacent matrix, but growth slowed sharply, especially in the cropland location.

354   The aspect of the curves does not suggest increases in richness at the location

355   scale on the sole basis of the inclusion of a drove road. The composition of the

356   drove road communities also showed no substantial differences from the

357   cropland and rangeland matrices. It is important to note that although the study

358   locations are still managed extensively, they are increasingly being replaced by

359   more common intensive schemes, and also that ants are sensitive to

360   agricultural and grazing intensification (Wilson et al., 1999; Andersen et al.,

361   2002; Philpott and Armbrecht, 2006). Thus, drove roads within these intensively

362   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

383 **Acknowledgements**

384

390   **References**

391

392   Alonso, L.E., Agosti, D., 2000. Biodiversity studies, monitoring and ants: an

393   overview, in: Agosti, D., Majer, J.D., Alonso, L.E. Schultz, T.R. (Eds.),

394   Standard Methods for Measuring and Monitoring Biodiversity.

395   Smithsonian Institution Press, Washington, District of Columbia, pp. 1-8.

396   Andersen, A.N., 1995. A classification of Australian ant communities based on

397   functional-groups which parallel plant life-forms in relation to stress and

398   disturbance. Journal of Biogeography 22, 15-29.

399   Andersen, A.N., Fisher, A., Hoffmann, B.D., Read, J.L., Richards, R.,2004. Use

400   of terrestrial invertebrates for biodiversity monitoring in Australian

401   rangelands, with particular reference to ants. Austral Ecology 29 87-92.

402   Arnan, X., Rodrigo, A., Molowny-Horas, R., Retana, J.,2010. Ant-mediated

403   expansion of an obligate seeder species during the first years after fire.

404   Plant Biology 12, 842-852.

405   Atauri, J.A., de Lucio, J.V.,2001. The role of landscape structure in species

406   richness distribution of birds, amphibians, reptiles and lepidopterans in

407   Mediterranean landscapes. Landscape Ecology 16, 147-159.

408   Azcarate, F.M., Peco, B.,2003. Spatial patterns of seed predation by harvester

409   ants (Messor Forel) in Mediterranean grassland and scrubland. Insectes

410   Sociaux 50, 120-126.

411   Azcarate, F.M., Peco, B.,2006. Effects of seed predation by ants on

412   Mediterranean grassland related to seed size. Journal of Vegetation

413   Science 17, 353-360.

414   Azcarate, F.M., Peco, B.,2007. Harvester ants (Messor barbarus) as

415   disturbance agents in Mediterranean grasslands. Journal of Vegetation

416   Science 18, 103-110.

417   Azcarate, F.M., Peco, B., 2012. Abandonment of grazing in a mediterranean

418   grassland area: consequences for ant assemblages. Insect Conservation

419   and Diversity 5, 279-288.

420   Azcárate, F.M., Robleño, I., Seoane, J, Manzano, P, Peco, B. (2012). Drove

421   roads as local biodiversity reservoirs: effects on landscape pattern and

422   plant communities in a Mediterranean region. Applied Vegetation

423   Science. DOI: 10.1111/avsc.12003

424   Bestelmeyer, B.T., Wiens, J.A.,1996. The effects of land use on the structure of

425   ground-foraging ant communities in the Argentine Chaco. Ecological

426   Applications 6, 1225-1240.

427   Bihn, J.H., Gebauer, G., Brandl, R.,2010. Loss of functional diversity of ant

428   assemblages in secondary tropical forests. Ecology 91, 782-792.

429   Boulton, A.M., Davies, K.F., Ward, P.S.,2005. Species richness, abundance,

430   and composition of ground-dwelling ants in northern California

431   grasslands: Role of plants, soil, and grazing. Environmental Entomology

432   34, 96-104.

433   Brown, W.L.,2000. Diversity of ants, in: Agosti, D. Majer, J.D., Alonso, L.E.,

434   Schultz, T.R. (Eds.), Ants. Standard Methods for Measuring and

435   Monitoring Biodiversity. Smithsonian Institution Press, Washington,

436   District of Columbia, pp. 45-79.

437   Bunce, R.G.H., De Aranzábal, I., Schmitz, M.F., Pineda, F.D.,2006. A review of

438 the role of Drove Roads (Cañadas) as Ecological Corridors. Alterra-

439 Rapport, Wageningen.

440 Cadotte, M.W., Carscadden, K., Mirotchnick, N.,2011. Beyond species:

441 functional diversity and the maintenance of ecological processes and

442 services. Journal of Applied Ecology 48, 1079-1087.

443 Cerda, A., Jurgensen, M.F.,2008. The influence of ants on soil and water losses

444 from an orange orchard in eastern Spain. Journal of Applied Entomology

445 132, 306-314.

446 Chen, Y.Q., Li, Q., Chen, Y.L., Lu, Z.X., Zhou, X.Y.,2011. Ant diversity and bio-

447 indicators in land management of lac insect agroecosystem in

448 Southwestern China. Biodiversity and Conservation 20, 3017-3038.

449 Crist, T.O.,2009. Biodiversity, species interactions, and functional roles of ants

450 (Hymenoptera: Formicidae) in fragmented landscapes: a review.

451 Myrmecological News 12, 3-13.

452 Dauber, J., Wolters, V.,2004. Edge effects on ant community structure and

453 species richness in an agricultural landscape. Biodiversity and

454 Conservation 13, 901-915.

455 Debussche, M., Lepart, J., Dervieux, A., 1999. Mediterranean landscape

456 changes: evidence from old postcards. Global Ecology and

457 Biogeography 8, 3-15.

458 Duelli, P.,1997. Biodiversity evaluation in agricultural landscapes: An approach

459 at two different scales. Agriculture Ecosystems & Environment 62, 81-91.

460 Folgarait, P.J.,1998. Ant biodiversity and its relationship to ecosystem

461 functioning: a review. Biodiversity and Conservation 7, 1221-1244.

462 Fourcassie, V., Dahbi, A., Cerda, X., 2000. Orientation and navigation during

463   adult transport between nests in the ant Cataglypis iberica.

464   Naturwissenschaften 87, 355-359.

465   Jones, J.C., Oldroyd, B.P., 2007. Nest thermoregulation in social insects.

466   Advances in Insect Physiology 33, 153-191.

467   Kaspari, M., Alonso, L., O'Donnell, S., 2000. Three energy variables predict ant

468   abundance at a geographical scale. Proceedings of The Royal Society B-

469   Biological Sciences 267, 485-489.

470   Laliberte, E., Legendre, P.,2010. A distance-based framework for measuring

471   functional diversity from multiple traits. Ecology 91, 299-305.

472   MacMahon, J.A., Mull, J.F., Crist, T.O.,2000. Harvester ants (Pogonomyrmex

473   spp.): Their community and ecosystem influences. Annual Review of

474   Ecology and Systematics 31, 265-291.

475   Mangas Navas, J.M.,1992. Cuadernos de la Trashumancia nº 0. Vías

476   Pecuarias. ICONA, Madrid.

477   Manzano, P., Casas, R.,2010. Past, present and future of Trashumancia in

478   Spain: nomadism in a developed country. Pastoralism 1, 72-90.

479   Manzano, P., Malo, J.E.,2006. Extreme long-distance seed dispersal via sheep.

480   Frontiers in Ecology and the Environment 4, 244-248.

481   Merino García, J., Alier Gándaras, J.L.,2004. La multifuncionalidad de las vías

482   pecuarias españolas en el marco del desarrollo rural. Tecnología y

483   desarrollo 2, 3-26.

484   O'Flanagan, P., Martinez, T.L., Abad, M.P.E.,2011. Restoration of sheep

485   transhumance In the Ebro Valley, Aragon, Spain. Geographical Review

486   101, 556-575.

487   Ordonez, J.L., Retana, J.,2004. Early reduction of post-fire recruitment of Pinus

488   nigra by post-dispersal seed predation in different time-since-fire

489   habitats. Ecography 27, 449-458.

490 Oteros–Rozas, E., González, J.A., Martín–López, B., López, C.A., Montes,

491   C.,2012. Ecosystem services and social–ecological resilience in

492   transhumance cultural landscapes: learning from the past, looking for a

493   future, in: T. Plieninger, T., Bieling, C. (Eds.), Resilience and the cultural

494   landscape: understanding and managing change in human–shaped

495   environments: Cambridge University Press.

496 Philpott, S.M., Armbrecht, I.,2006. Biodiversity in tropical agroforests and the

497   ecological role of ants and ant diversity in predatory function. Ecological

498   Entomology 31, 369-377.

499 Read, J.L., Andersen, A.N.,2000. The value of ants as early warning

500   bioindicators: responses to pulsed cattle grazing at an Australian arid

501   zone locality. Journal of Arid Environments 45, 231-251.

502 Remm, J., Lohmus, A., 2011. Tree cavities in forests - The broad distribution

503   pattern of a keystone structure for biodiversity. Forest Ecology and

504   Management 262, 579-585.

505 Ries, L., Fletcher, R.J., Battin, J., Sisk, T.D., 2004. Ecological responses to

506   habitat edges: Mechanisms, models, and variability explained. Annual

507   Review of Ecology Evolution and Systematics 35, 491-522.

508 Roig, X., Espadaler, X.,2010. Propuesta de grupos funcionales de hormigas

509   para la Península Ibérica y Baleares, y su uso como bioindicadores.

510   Iberomyrmex 2, 28-29.

511 Ruiz, M.,2001. The ecological and economical rationale for transhumance

512   practices in Spain. Wageningen, The Netherlands.

513 Ruiz, M., Ruiz, J.P.,1986. Ecological History of Transhumance in Spain.

514   Biological Conservation 37, 73-86.

515 Silva, R.R., Brandao, C.R.F.,2010. Morphological patterns and community

516   organization in leaf-litter ant assemblages. Ecological Monographs 80,

517   107-124.

518 Sobrinho, T.G., Schoereder, J.H.,2007. Edge and shape effects on ant

519   (Hymenoptera : Formicidae) species richness and composition in forest

520   fragments. Biodiversity and Conservation 16, 1459-1470.

521 Steiner, F.M., Schlick-Steiner, B.C.,2004. Edge effects on the diversity of ant

522   assemblages in a xeric alluvial habitat in central Europe (Hymenoptera :

523   Formicidae). Entomologia Generalis 27, 55-62.

524 Szczepko, K., Kruk, A., Bartos, M.,2012. The role of mosaicity of the post-

525   agriculture area of the Kampinos National Park in determining the

526   diversity of species of spider wasps (Hymenoptera: Pompilidae).

527   European Journal of Entomology 109, 35-46.

528 Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M.,

529   Jeltsch, F.,2004. Animal species diversity driven by habitat

530   heterogeneity/diversity: the importance of keystone structures. Journal of

531   Biogeography 31, 79-92.

532 Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E.,1997. The

533   influence of functional diversity and composition on ecosystem

534   processes. Science 277, 1300-1302.

535 Underwood, E.C., Fisher, B.L.,2006. The role of ants in conservation

536   monitoring: If, when, and how. Biological Conservation 132, 166-182.

537 Wilson, J.D., Morris, A.J., Arroyo, B.E., Clark, S.C., Bradbury, R.B.,1999. A

538   review of the abundance and diversity of invertebrate and plant foods of

539   granivorous birds in northern Europe in relation to agricultural change.

540   Agriculture Ecosystems & Environment 75, 13-30.

541   Wolff, A., Debussche, M.,1999. Ants as seed dispersers in a Mediterranean old-

542   field succession. Oikos 84, 443-452.

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 & *Soils*	T & *P*	Predominant Matrix
Cropland	Quijorna (Cañada Real Segoviana)	600	Arkose *Luvisols, Cambisols*	14.5ºC *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*	13.0ºC *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*	11ºC *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*	6-9ºC *800-1500 mm*	Forests dominated by *Pinus sylvestris* L., used for logging and occasional grazing.

545 Table 2. Functional traits used to obtain the functional diversity index FDis, and

546 weights assigned to each variable. FDis was calculated as the mean distance in

547 a multidimensional trait space of individual species from the centroid of all

548 species in an assemblage. The variables were weighted to place all three sets

549 (functional groups, biometrics and trophic niche descriptors) on an equal

550 footing.

551

Set of variables	Type	Variables	Weight in FDis	
Functional Group	Categorical	Cryptic	1/12	
		Cold Climate & Shade Specialists	1/12	
		Generalists & Opportunists	1/12	1/3
		Hot Climate & Open Habitat Specialists	1/12	
Trophic Niche	Categorical (non-exclusive)	Seeds	1/12	
		Nectar	1/12	1/3
		Animal remains	1/12	
		Aphids	1/12	
Biometry	Continuous	Eye length	1/15	
		Femur length	1/15	
		Tibia length	1/15	1/3
		Head length	1/15	
		Head width	1/15	

552

553

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

558

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 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]

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.
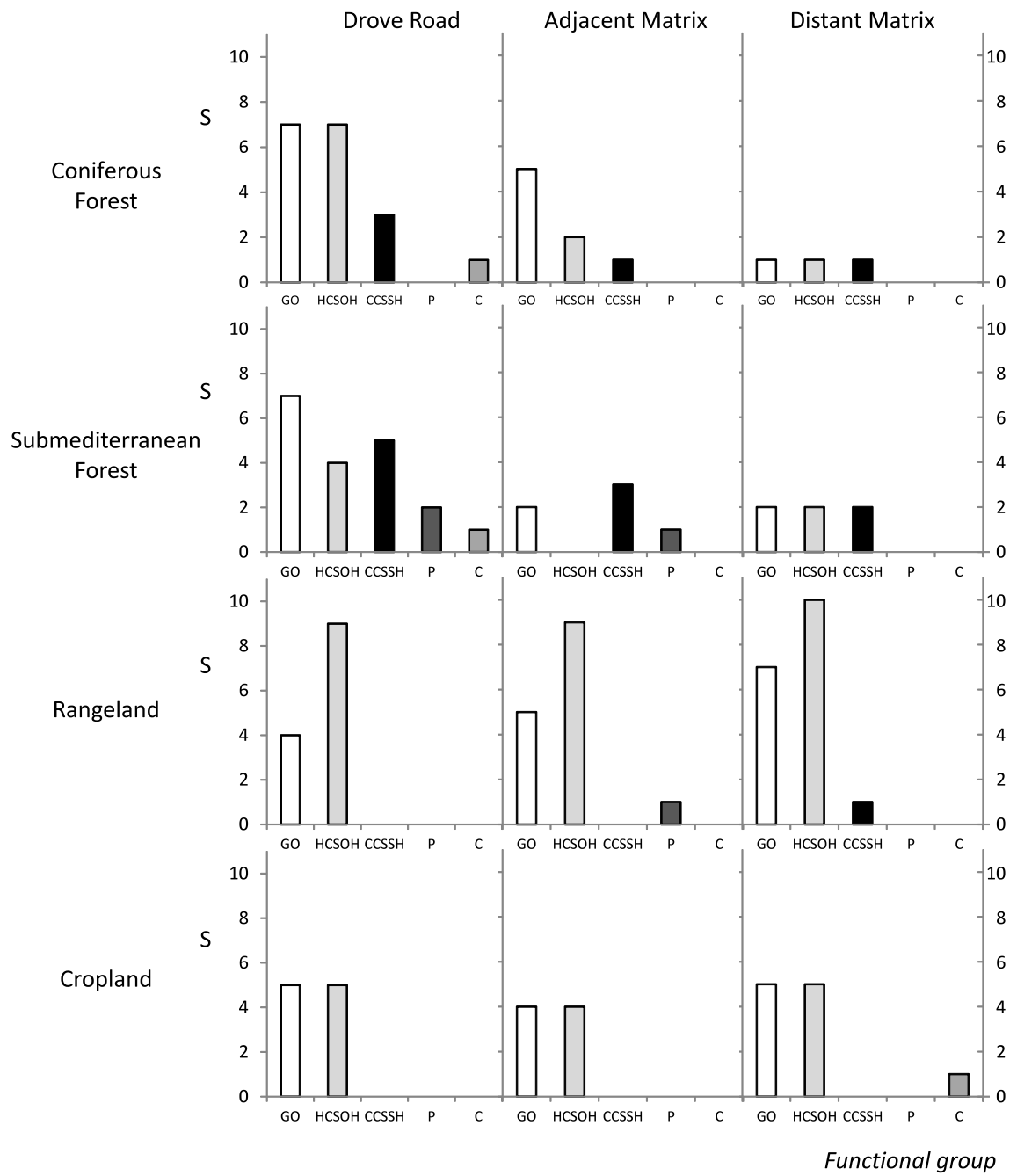
Figure 4. Species accumulation curves of the four study locations, constructed by combining the accumulation due to the three different habitat types. Data points for each part of the curve show mean species richness (y-axis) for a certain number of sampling units (x-axis) with all possible sampling orders.

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

588

Figure 1.

589

590

591

Figure 2.

Coniferous Forest

Submediterranean Forest

Rangeland

Cropland
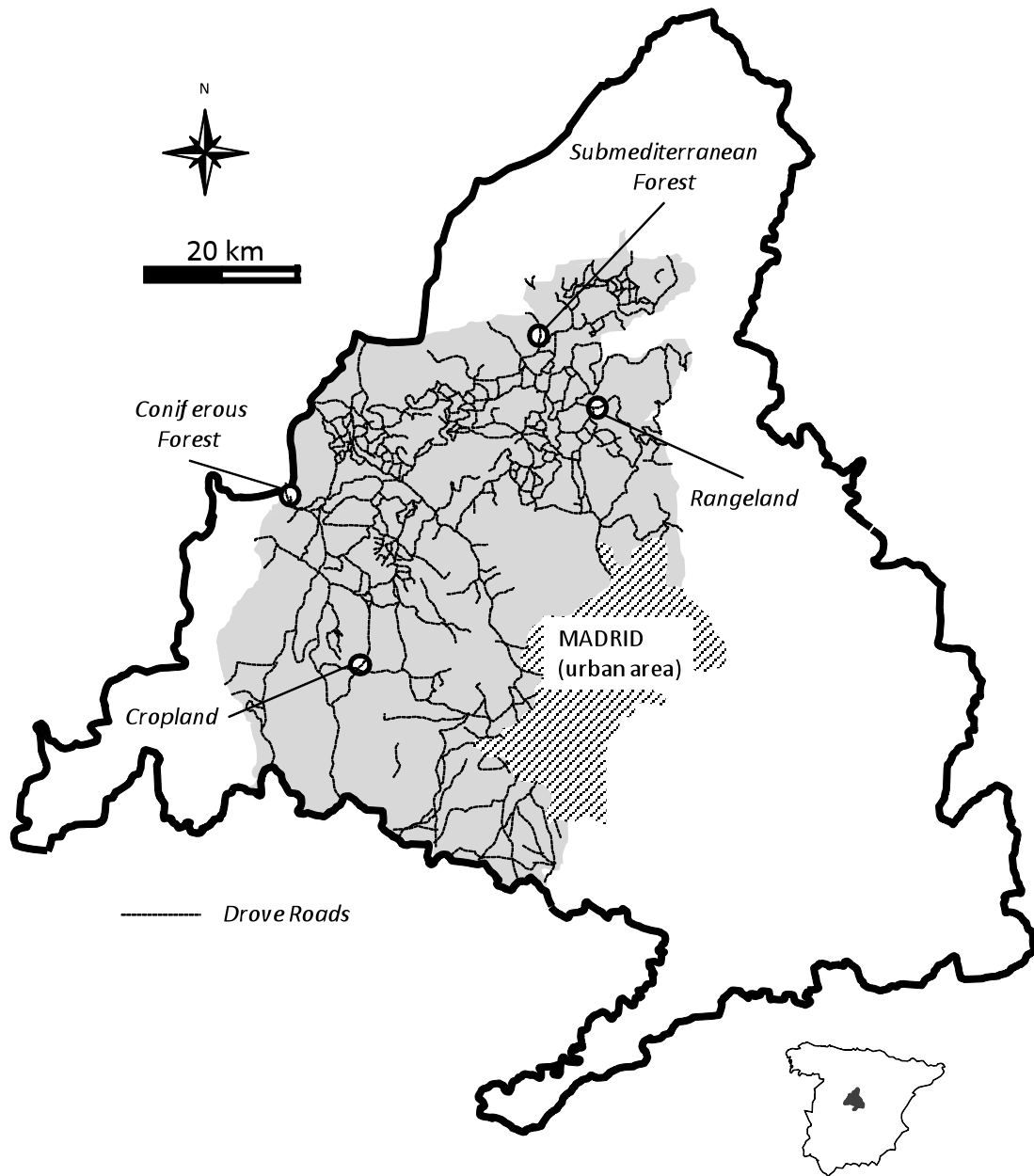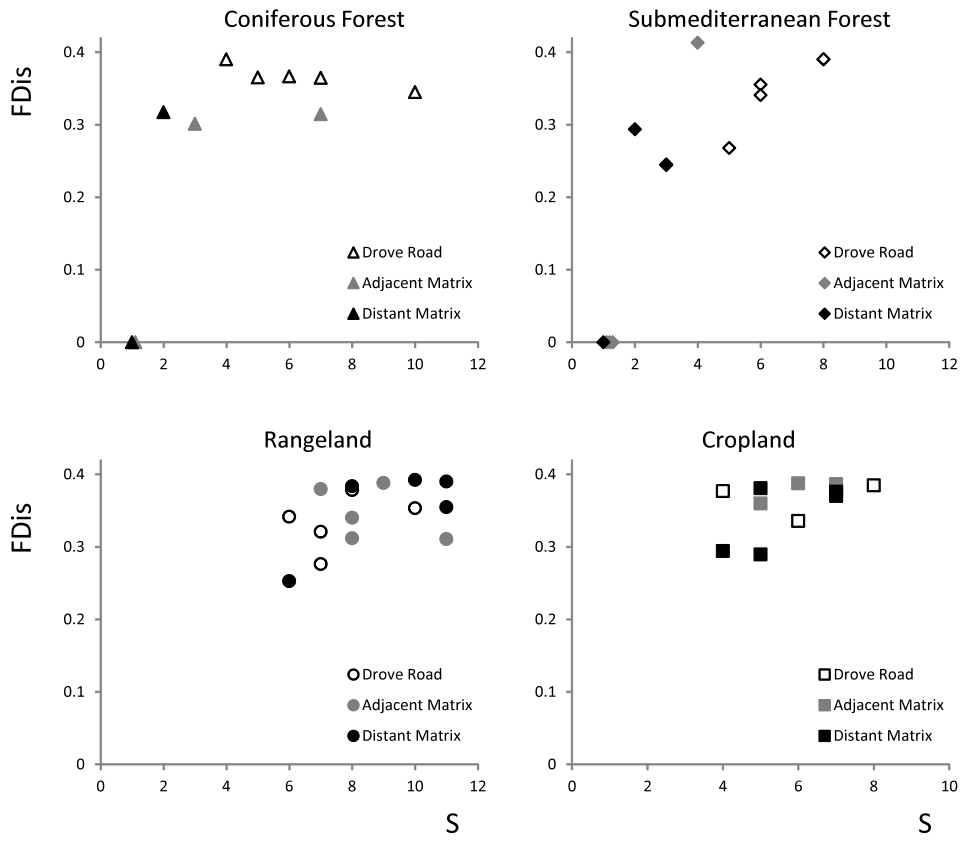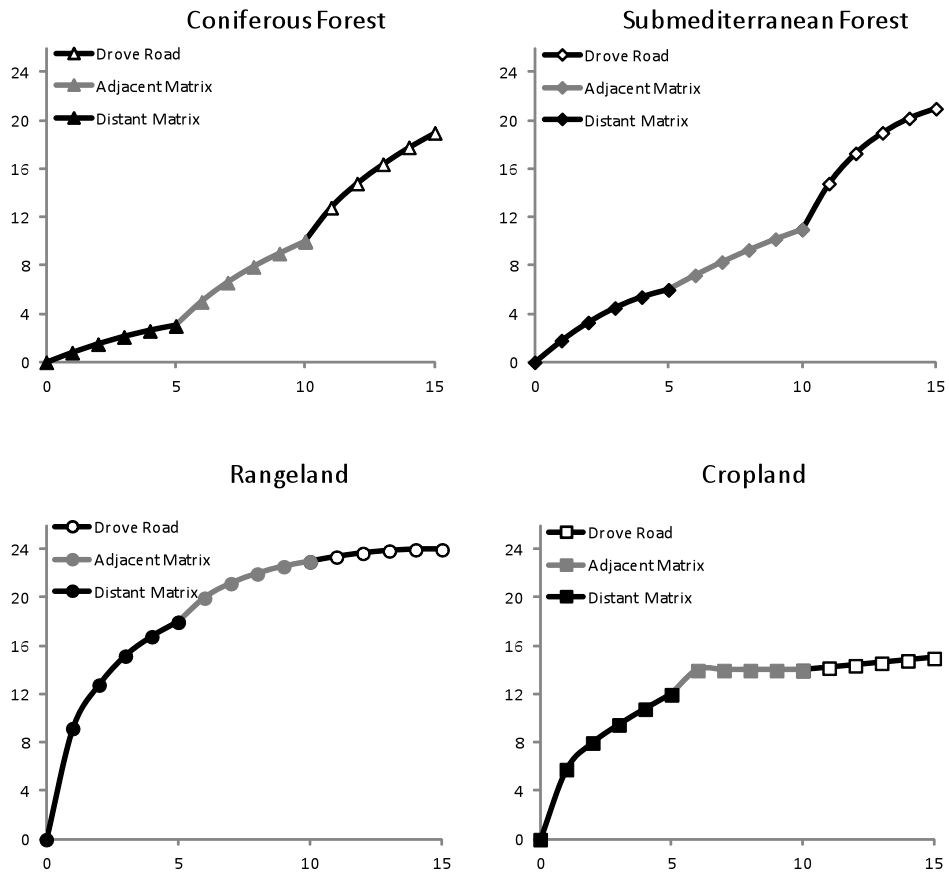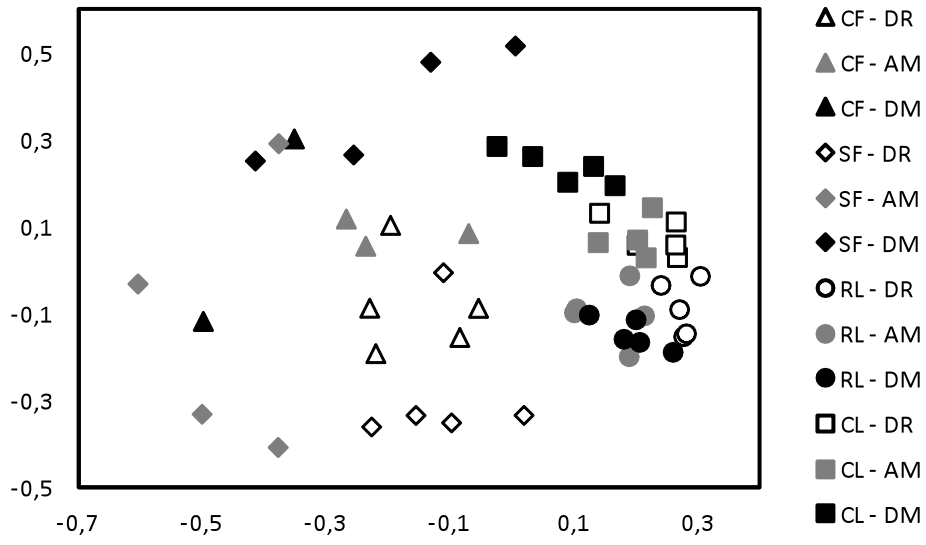
593

594

595   Figure 3.

596

597

598   Figure 4.

599

600

601   Figure 5.

602