Stream distance and vegetation structure are among the major factors affecting various groups of arthropods in non-riparian chestnut forests

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Abstract

Streams are likely to be increasingly important for the conservation of non-riparian forest diversity with increased aridity due to climate change in many parts of the world. However, the importance of streams as promoters of non-riparian forest diversity has not been explored in detail. Given the likely stronger effect of surrounding habitats on open forests, we examined chestnut woodlands in northern Spain ($n = 32$) to explore the contribution of streams to variation in arthropod measures. We captured 5,490 arthropods (21 orders and 63 families) from which we calculated total abundance and richness and the abundance of trophic guilds. Vegetation structure at the tree and understory levels often made the largest independent contributions to explained variation in arthropod numbers and effects suggested alterations in arthropods' food-web. Negative effects of stream-distance on taxon richness and the abundance of predators, omnivores and phytophages seemed to be largely mediated by vegetation structure. The exception was a strong univariate inverse association between the abundance of aerial predators and stream distance, possibly because wasps might be exploiting riverine habitats. Overall, effects of stream-distance were weaker for ground than for aerial arthropod groups. Moreover, arthropod numbers were greater at sites with low tree species richness and tall and species-rich understories, raising concerns for the ecological consequences of the abandonment of traditional forest practices in these woodlands. Gains in arthropod diversity and ecosystem services (e.g. pest control, nutrient cycling, pollination) might be had if non-riparian forests are managed in a way that depends on stream-distance. Inferences may improve with a more complete knowledge of the biology of poorly studied groups, such as flies.

Keywords: arthropods; trophic guilds; rural abandonment; tree richness; understory development; leaf litter; streams; woodlands; old-growth trees;

1. Introduction

Climate, geomorphology and human activities determine the structure of extant forests around the world (Ellis, 2015; Ghazoul and Chazdon, 2017), and temperate deciduous forests are among the most human altered (Gilliam, 2016). Logging and land clearing for agriculture have degraded these forests for centuries, but relatively recent human movements from rural areas to cities has led to forest regeneration in parts of Europe and North America (Malavasi et al., 2018). Not only have forests increased in area in Europe (Navarro and Pereira, 2015), but what have been open forests have become denser and structurally more complex, with high tree densities and well-developed understories (Spitzer et al., 2008; Malavasi et al., 2018). Although structural complexity often promotes biodiversity (Paillet et al., 2010), shading in older or dense forests may reduce understory diversity (Kovac et al., 2018). Therefore, the chronosequences of forests with different structural complexity provides an opportunity to identify the main promoters and modulators of biodiversity (Vesk et al., 2008).

Temperate deciduous forests often are in regions with warm, moist summers and cool winters (Gilliam, 2016), so that the maintenance of moisture during mild seasons might be an important factor for the conservation of their biodiversity (Fig. 1). Moisture in forests depends on the ability of trees to maintain humidity and to channel water from rain and fog to the soil, all of which are associated with canopy and tree density (Barbier et al., 2009). High leaf-litter biomass and well-developed understories retain soil moisture and humidity (Gilliam, 2007). Streams provide terrestrial ecosystems with water and other benefits, including more habitat diversity and being corridors for fauna (Ramey and Richardson, 2017; Selwood et al., 2017). However, the importance of streams as promoters of biodiversity has been studied mostly in riparian habitats (e.g. Maceda-Veiga et al., 2016; Paredes et al., 2017; Suri et al., 2017). Terrestrial and aquatic systems exchange nutrients, energy and biota (Marczak et al., 2007; Ramey and Richardson, 2017). Distance from streams is often used as covariate in studies on terrestrial species (e.g. Paredes et al., 2017). However, the relative contribution of streams to the diversity of non-riparian forests or woodlands has not been explored in detail, which limits our ability to assess the potential of streams to mitigate increased aridity on terrestrial ecosystems due to climate change (Garcia et al., 2014).

Studies addressing trophic guilds can provide useful insights into this question because forest-vegetation structure and streams may affect basal resources available to consumers (Likens and Bormann, 1974; Blondel, 2003). Changes in vegetation structure

88   and stream distance also can alter forest microclimate (e.g. moisture, temperature)

89   thereby influencing ecosystem processes (e.g. the organic matter cycle, Gilliam et al.,

90   2014). Changes in forest conditions therefore can directly or indirectly affect many

91   forest organisms (Allen, 2016), but effects of alterations in trophic resources are

92   expected to be small for omnivores or decomposers due to their wide trophic spectrum

93   (Setälä et al., 2005). While predators can be generalist consumers, they may be

94   particularly affected because of dependence on the structure of the entire food-web

95   (Duffy, 2003; Tews et al., 2004). Nonetheless, many factors can affect the trophic guild

96   structure of consumers, including the complexity of food-webs (Setälä et al., 2005) and

97   consumers' mobility, with highly mobile animals probably less affected than more

98   sedentary taxa.

99   Arthropods are key taxa for exploring the ecological effects of alterations in

100   forest-vegetation structure because they are species rich and have diverse ecological

101   strategies (e.g. flying, detritivores, predators) (Stork, 2018; Yang and Gratton, 2014).

102   Moreover, arthropods' life-history, and so the ecosystem processes where they act (e.g.

103   leaf-litter breakdown, Setäla et al., 2005), are sensitive to changes in microclimatic

104   conditions (A'Bear et al., 2014; Dray et al., 2014). As far as we are aware, no study has

105   explored how changes in vegetation structure and stream distance affect taxon richness

106   and the trophic guild structure of non-riparian arthropod assemblages. However, these

107   arthropod measures are likely to be suitable for assessing the links between non-riparian

108   forests and streams because arthropods are sensitive to changes in forest-vegetation

109   structure and microclimate (e.g. Jabin et al., 2004; Dauber et al., 2005; Allen, 2016;

110   Maceda-Veiga et al., 2016).

111   We trapped several groups of arthropods in northwestern Spain to explore the

112   links between streams and non-riparian chestnut (*Castanea sativa* Miller, 1768) forests.

113   Streams shape many temperate forests and woodlands around the world (Likens and

114   Bormann, 1974; Mills, 1980) and forests in this region are no exception (García et al.,

115   2014). The focal chestnut woodlands are typical examples of rural abandonment and

116   fragmentation, two threats affecting other temperate deciduous woodlands especially in

117   Europe and North America (Miklín and Čížek, 2014; Gilliam, 2016; Sebek et al., 2016).

118   We expected stream distance to be an important factor in forest management if there are

119   clear associations with arthropods after accounting for the effects of other determinants

120   of forest diversity (Table 1). If so, we expected stream effects to be particularly

121   important in open chestnut forests compared to more close ones because low structural

122 vegetation development should provide fewer resources for arthropods (Fig. 1).

123 Moreover, structural vegetation development should be negatively associated with

124 arthropods if arthropods benefit from the conditions promoted by rural abandonment.

125

126 **2. Materials and methods**

127 *2.1. Study area*

128   We surveyed 32 chestnut forest patches near to the Sites of Community

129 Importance 'SCI ES1120016 Río Cabe' and 'ES1120001 Ancares-Courel' in

130 northwestern Spain (Habitats Directive 92/43/EEC, Fig. 2). Located in the municipality

131 of O Incio, the study area (19 km^2) is sparsely populated (c. 300 inhabitants), is far from

132 industries (>30 km) and has little ranching (c. 80 head of cattle). Air quality is good

133 gauging from the structure of epiphytic lichen assemblages (Maceda-Veiga and Gómez-

134 Bolea, 2017). The climate is temperate oceanic sub-Mediterranean (Rivas-Martínez,

135 2004): fog is frequent, there is abundant rain (800-1800 mm annual), and the average

136 annual temperature is 16°C, but summers can be dry and warm (<60mm; >27°C).

137   The management of chestnut forests consists of pruning trees in winter and an

138 annual manual clear of the undergrowth at summer's end to facilitate harvesting

139 chestnuts in autumn. All sampling sites were on individually managed private

140 properties, which has led to a wide variation in forest structures depending on the

141 degree of 'abandonment' (Fig. 1, Appendix S1). The dominant forest species in the

142 study area are chestnuts followed by native oaks (*Quercus robur* and *Q. pyrenaica*).

143 Open lands consist of grasslands, shrublands and seldom small orchards. Streams

144 (Strahler number = 1-2) and secondary roads with little traffic (e.g. 1 car/5 h) cross the

145 study area. The water quality in streams is good (Conductivity = 102-304 µS/cm, pH =

146 7.5-8, NH_4 < 0.2 mg/l; A.M.V. *unpublished data*).

147

148 *2.2. Forest patch characteristics: stream distance, vegetation and covariates*

149   We measured the distance to the nearest stream for each sampling site and other

150 25 predictors and covariates that might affect arthropod assemblages. Arthropod traps

151 (see the description in section 2.3.) were placed in the centre of 32 forest patches, from

152 which we obtained the 26 measurements described in Appendix S2 in detail and that are

153 outlined briefly below.

154   *Structural development of vegetation* was characterized for the tree (i.e.

155 measures of tree density, tree species richness, tree size and number of standing dead

156 trees) and understory levels (understory cover, understory species richness and

157 understory height). Dead litter biomass and deadwood cover were other indicators of

158 vegetation development in each sampling site, while the C and N stable isotope ratios

159 was used as measures of litter quality and degree of decomposition. All predictors can

160 be regarded as informing *forest-microclimatic condition*s, although we measured light

161 intensity, temperature and litter moisture in all sampling sites (Appendix S2).

162   The covariates in our study were the spatial distribution of sampling sites (i.e.

163 spatial correlations), the size and shape of forest patches and the type of vegetation

164 around each private property. We included the distance from each sampling site to the

165 centroid (median of all *UTM-X* and *UTM-Y*), elevation (m.a.s.l.) and slope in analyses.

166 Patch shape was calculated using the shape index $= p/2*(\pi \cdot a)$ (Lang and Blaschke,

167 2007), where p is the perimeter and a is the area of each sampling site as indicated in

168 the Spanish record of forest properties (the 'Sigpac' visor). The surrounding vegetation

169 was estimated within 500 m of each arthropod trap by recording the percentage of the

170 surface with chestnut forest, other deciduous trees, pines, grasslands, shrublands, urban

171 areas, secondary roads and other land uses (e.g. orchards). Other radii (100 and 1000 m)

172 were less informative than 500 m in the study area (see Appendix S3).

173 *2.3. Arthropod sampling*

174   We set two types of pitfall traps from the 2nd to the 19th August 2017 (18 days in

175 the boreal summer) to improve the likelihood of capture of arthropods with different

176 mobilities and feeding strategies. Crawling arthropods were captured using ground

177 pitfall traps, which mostly capture ground predators (Sabu et al., 2011). We placed a

178 500-ml polyethylene container (10 cm diameter) with a funnel, filled with concentrated

179 sea salt solution as the preservation agent as described in Maceda-Veiga et al. (2016).

180 Several groups of flying insects were caught using a modified version of the widely

181 used beer trap (Dvorák et al., 2010; Manko et al., 2018); we placed a 200-ml

182 polyethylene container (5 cm diameter) with a funnel, filled with Estrella Galicia$^{®}$ beer,

183 vinegar, and sugar as a bait (Carles-Tolrá et al., 2017). The container had a lid with a U-

184 shape to prevent rain from entering the trap. We hung the traps on a tree branch at c. 1.5

185 m from the ground and at c. 40 m from the trunk. In our pilot study we found that this

186 bait attracted some predators (e.g. social and parasitic wasps, scorpion flies) and several

187 groups of decomposers and fermented liquid feeders (e.g. Nitidulidae, Staphylinidae,

188 Heleomyzidae, Muscidae, Drosophilidae, Sarcophagidae; A.M.V. & M.C.T.

189 unpublished data). Therefore, this trap was suitable for exploring how changes in forest-

190 microclimatic conditions may have affected the microbial-driven process of

191 fermentation, and hence, the dependent insects (e.g. Becher et al., 2012). Our bait trap

192 was not occluded by similar food items in the focal forests during the surveys (e.g.

193 decaying fruits or mushrooms). We emulated the presence of ephemeral and patchy

194 resources as do dung and carrion traps for insects (Braack, 1987; Gibbs and Stanton,

195 2001).

196   Owners allowed us to set only one trap for flying insects and one for ground

197 arthropods at the centre of each private property. In the pilot study, we set three pitfall

198 traps spaced 20 m apart in four of the studied sites and mean±SD arthropod richness and

199 abundance were 17±2.5 and 75±25, respectively (Appendix S4). Moreover, we

200 measured patch features for each trap location, calculated estimated species richness and

201 included patch size as covariate (see section 2.4.). All arthropods from each trap were

202 preserved in a single pot with 70% ethanol and were identified in the laboratory to the

203 lowest taxonomic possible level (Appendix S5). The proportions of individuals

204 identified to species level were similar among sites (e.g. mean±SD = 0.38±0.09). All

205 individuals of families identified by taxonomic experts were identified to species level

206 and assigned to an adult trophic guild based on literature, mouth morphology, and

207 authors' personal observations (Appendix S5). For taxa not identified to species level,

208 we recorded the family as an additional 'species' in richness measures if no other

209 individuals classified to species level was from that family in a sample.

210 *2.4. Statistical analyses*

211   The associations with vegetation structure and stream distance were assessed

212 separately for soil and flying arthropods. The response variables were abundance and

213 observed and estimated species richness. We used the Chao1 species-richness estimator

214 to explore the possible effects of the incompleteness of species inventories based on

215 how species detection varied as function of differences in arthropod captures across

216 sampling sites (Walther and Moore, 2005). For greater analytical sensitivity, gradients

217 of variation in forest-patch characteristics were used in analyses rather than categorizing

218 forest patches (e.g. more or less abandoned).

219

2.4.1. Data transformations and dealing with collinearity among predictors

All analyses were conducted in R (R Core Team, 2018) using the functions outlined below. The distributions of all predictors were visually inspected and, where necessary, transformations were made to make the predictors more normally distributed (e.g. log for all continuous variables). Understory cover was transformed into a categorical variable with three levels (0%, 1-75%, and >75%) and deadwood into presence or absence data because the usual recommended transformations for this type of data were ineffective. Predictors were standardized using the R function *scale* to be expressed on units of standard deviation of the respective predictors.

Collinearity causes instability in parameter estimation in linear models (Harrell, 2015). Therefore, the 26 predictors were examined for shared variance using the function *vif* in the package *usdm* (Naimi, 2015) using a threshold of ≤ 3, a value recommended by Zuur et al. (2010). Spearman-rank correlation coefficients among omitted and selected variables according to VIF are shown in appendices S1 and S6 and a rationale for each retained predictor is provided in Table 1.

2.4.2. General linear models and hierarchical partitioning

Inspection of the distributions of the response variables (for ground and aerial traps separately) indicated that abundance had a log-Gaussian distribution and that richness had a Poisson distribution.

Variation in arthropod measures as function of forest-patch characteristics was examined using generalized lineal models (GLMs) and analyses of hierarchical partitioning (HP). Standardized regression coefficients of GLMs (the R function *glm* in the package *MASS*, Ripley et al., 2013) indicated the direction and magnitude of the associations between forest patches and arthropods. HP analysis (the R function *hier.part* in the package *hier.part*, Walsh and Mac Nally, 2015) was used to compute the independent explained variances by individual predictors and covariates in GLMs while accounting for residual collinearity among predictors (Mac Nally, 2000).

The initial GLM for all response variables and arthropod groups accounted for the effects of stream distance and all predictors related to structural vegetation development, forest microclimatic conditions and covariates from Appendix S6. Initial GLMs also included the interactions of stream distance with litter biomass, tree density, understory height and understory cover to explore whether the effects of stream distance depended on structural vegetation development. The most relevant predictors among all

253 possible combinations in GLMs explaining variation in response variables were

254 identified using the function *dredge* in the package *MuMin* (Barton, 2018). A summary

255 model based on model averaged coefficients of the 'best' models (Akaike Information

256 Criterion corrected for small sample sizes, AICc ≤ 2) was computed using the R

257 function *model.avg* in the package *MuMIn*. Overall fit for the averaged model was

258 calculated as: [null deviance-residual deviance]/null deviance (i.e. % explained

259 deviance) (Mac Nally et al., 2018). Diagnostic plots of model residuals showed that the

260 statistical assumptions of normality, homogeneity of variances and the presence of

261 unduly observations were met (Zuur et al., 2010).

262 There would be support for the expectation that streams might be important for

263 explaining variation in non-riparian arthropod data if the final GLMs included additive

264 or interactive effects for stream distance and their effect sizes (± 95% confidence

265 intervals, CI) excluded zero. The individual importance of the predictors identified by

266 GLMs was also assessed using HP analyses and statistical significance was gauged

267 based on the upper 95% confidence interval using permutation tests with 999

268 permutations (the R function *rand.hp*, Walsh and Mac Nally, 2015).

269

270 **3. Results**

271 The 32 forest properties spanned spatial gradients of structural development of

272 vegetation and stream distance (Appendix S1). Stream distance was poorly correlated

273 with measures of structural development of vegetation (understory height Spearman's ρ

274 = 0.03; understory cover, ρ = 0.15; litter biomass, ρ = 0.03; tree density, ρ = 0.15; P >

275 0.05), so that their interactive effects with stream distance could be explored. Tree

276 density was negatively associated with tree perimeter (ρ = 0.60; P < 0.05) and was

277 positively associated with understory height (ρ = 0.48; P < 0.05), reflecting the vertical

278 development of vegetation in unmanaged chestnut woodlands.

279

280 Ground traps captured 1,666 individuals from 6 classes and 16 orders, while aerial traps

281 snared 3,824 specimens from 5 orders and 40 families (Table 2, Appendix S5). Ground

282 arthropods belonged to four adult trophic guilds and aerial captures were from three

283 trophic guilds (Appendix S5). Ground traps mostly captured predators and omnivores,

284 while aerial traps mostly trapped omnivores. However, omnivory differed among trap

285 methods; omnivores were floral visitors and fermented-liquid feeders (e.g. decomposed

286 vegetables or animals) for aerial traps and hunters, occasionally frugivores and

287 decomposers of carrion or dead plants for ground traps.

288

289 *3.1. Models for total abundance and taxon richness*

290 The explained variances of the best-fitting GLMs for ground-trap data were from 0.47

291 to 0.62 and model fits for aerial-trap data were from 0.43 to 0.73 (Table 3). GLMs for

292 Chao-estimated richness in aerial and ground arthropods had the best model fits. GLMs

293 and HP models consistently showed that tree richness and density made the largest

294 individual contributions to explaining variation in ground-arthropod measures. For

295 aerial captures, understory height, litter biomass, stream distance and the type of land

296 uses surrounding the focal forest patches individually explained substantial variation in

297 HP analyses. However, the interactive effects between stream distance and some

298 vegetation variables (litter biomass and understory height or cover) were important for

299 the Chao-estimated richness in ground captures and for the three measures (abundance,

300 observed and Chao-estimated richness) in aerial captures (Table 3).

301   Overall, numbers of arthropods were associated positively with understory

302 height or cover, litter biomass or quality and tree abundance (Table 3, Fig. 3). However,

303 associations between arthropods and tree richness or stream distance were negative

304 (Table 3, Fig. 3). The association between stream distance and ground captures changed

305 from negative to positive with greater litter biomass (Fig. 4). Taller understories

306 appeared to reduce the negative association of stream distance with aerial captures (Fig.

307 5). Conversely, the inverse association between stream distance and aerial captures was

308 accentuated by greater litter biomass (Fig. 4).

309

310 *3.2. Models for the abundance of trophic guilds*

311   The explained variances of GLMs for the trophic guilds of ground arthropods

312 were from 0.32 to 0.68 and model fits for flying insects were from 0.13 to 0.38 (Table

313 4). The best model fits were for the abundance of ground phytophages and aerial

314 predators (excluding parasitoids). Overall, the trophic guilds for ground arthropods were

315 more sensitive to forest-patch characteristics than those for flying insects (Table 4).

316 Stream distance was more influential in explaining variation in aerial arthropods

317 (negative association) than for ground arthropods.

318   Variation in the abundance of ground predators was due mostly to a negative

319 association with tree species richness and a positive association with the amount of open

space due to secondary roads. Variation in the abundance of aerial predators (excluding parasitoids) largely was due to a negative association with stream distance (Table 4). However, tall understory height was the most important factor in explaining the abundance of parasitoids (Table 4). While statistically weak, the abundance of aerial omnivores was negatively associated with stream distance and was positively related to litter biomass (Table 4). Conversely, the abundance of ground omnivores was significantly negatively associated with tree richness and positively associated with tree density (Table 4). Decomposers, which were only from ground traps, had a marked positive association with litter moisture (Table 4). Variation in the abundance of phytophages, also only from ground traps, was mostly positive associated with understory cover (Table 4).

The interactive effects between stream distance and tree density or understory height were important for phytophages, omnivores and predators (Table 4). The negative association between the abundance of phytophages and stream distance was accentuated by lower vegetation heights or greater tree densities (Appendix S7). The inverse association between litter biomass and the abundance of aerial omnivores was accentuated by greater stream distances. Last, greater understory heights seemed to partially offset the negative effects of stream distance on the abundance of aerial predators (Appendix S7).

4. Discussion

Our study provides insights into how the abundance and diversity of several groups of arthropods might benefit from different vegetation structures in non-riparian forests conditional on stream distance. The links between streams and non-riparian forests are largely unexplored compared to the many reports of links (e.g. exchanges of energy and biota) between streams and riparian habitats (Standford, 1998; Sabo and Power, 2002; Ramey and Richardson, 2017).

Stream distance was negatively associated with 66% of total arthropod measures, being the strongest effects for aerial captures in general, and with omnivores and predators (excluding parasitoids) in particular. However, these associations were reversed at sites with greater structural development of vegetation, probably due to less severe microclimates and the availability of more resources for arthropods. Chestnut woodlands further from streams probably are less humid and our results may have been exacerbated by surveys having been conducted in the summer of a particularly dry year

354 (33% less rain than the regional annual mean of 1,408.3 l/m^2). However, this amount of

355 drying may be common in future (Rodríguez-Puebla and Nieto, 2010; Garcia et al.,

356 2014), so the results are probably highly informative. Species of the most-recorded fly

357 families (e.g. Heleomyzidae, Lauxaniidae, Fanniidae, Drosophilidae) feed on decaying

358 plant and fungi (Hövemeyer, 2000; Krivosheina, 2008), and decomposition is

359 accelerated under humid conditions. Understory development is associated with forest

360 patches maintaining moister conditions (Gilliam, 2007; Parker et al., 2012). Therefore,

361 measures of vegetation structure might have reflected better the microclimatic regime

362 that arthropods experience than snap-shot measures of forest environmental conditions

363 (e.g. temperature, lighting). The positive association between understory height and

364 plant species richness suggested that inferences from microclimate may be partially

365 occluded by a greater diversity of resources for arthropods, which occur at sites with

366 high plant richness (e.g. shelter, food; Lawton, 1983; Haddad et al., 2009). If greater

367 understory height or cover increased the abundance of prey, the observed increases in

368 predator abundance then are to be expected.

369 Alongside indirect effects, the inverse association between stream distance and

370 aerial captures may be due to insects directly exploiting riverine habitats. The distance

371 between streams and focal forest patches ranged from 4 to 620 m, which is within the

372 flight range of many insects (e.g. Dew and Michener, 1978; Roitberg et al., 1984;

373 Stanfield and Hunter, 2009). Riparian habitats often had dead trunks with fungi (A.M.V.

374 observation), which are a foraging resource to often recorded omnivorous flies (e.g.

375 Drosophiliidae, *Phaonia pallida* (Fabricius, 1787); Papp, 2002; Chandler, 2010). Diets

376 of aerial predators (vespids and hornets) include chewed wood fibers and arthropods

377 occurring in riparian habitats (e.g. flies, spiders) (Harris, 1991; Beggs et al., 2011).

378 Hornets (e.g. *Vespa crabro* Linnaeus 1758) also might be able to build their nests in

379 chestnuts close to streams because humidity increases bark thickness (Stahl et al.,

380 2010). Last, captured flies and wasps might be using riparian corridors as flight paths;

381 forest roads ≤ 15 m are used by hoverflies in this way (Gittings et al., 2006), but this

382 question has not been investigated for dipterans and wasps in rivers.

383 Stream distance had the largest independent contribution to explained variation

384 in the abundance of aerial predators, but the individual contributions of tree or

385 understory features were more important for the other arthropod measures. For ground

386 arthropods, tree richness had the strongest (negative) association, notwithstanding high

387 plant richness often is associated with high arthropod diversity (Dinnage et al., 2012;

Sobek et al., 2009). However, tree richness in our study was a measure of poor chestnut-woodland condition. Other native trees (e.g. *Quercus robur*, *Prunus avium*) grow in unmanaged chestnut forests (Conedera et al., 2016), so that our study may add various groups of arthropods to the list of taxa that benefits from the maintenance of open old-growth chestnut woodlands (Guitián et al., 2012). Plantations of apple trees and poplar *Populus* spp., found in the focal forests with tree richness > 3, seemed to be particularly detrimental for ground arthropods, which is consistent with how sensitive ground arthropods are to alterations in the resources trees provide to soils (e.g. physical habitat, food) (Vehviläinen et al., 2008; Tedersoo et al., 2016). Increased tree density, which was mainly due to young chestnut trees, was associated positively with the abundance of ground omnivores. The most likely explanation for this finding is the preference of the most-recorded omnivores, wood crickets *Nemobious sylvestris* (Bosc, 1792), for open canopies (Brouwers and Newton, 2009), which are typical of young forests.

Understory development was particularly important for explaining variation in the abundance of aerial parasitoids and ground phytophages. Results for parasitoids support the broad evidence that diverse and tall understories promote insects important for natural pest control in agriculture and forestry (e.g. Ichneumonidae, Braconidae; Bugg and Waddington, 1994; Smith et al., 2015). Outcomes for ground phytophages showed the expected positive association with vegetation cover (Lawton, 1983), albeit the association was negative with understory height. The fern *Pteridium aquilinum* was common at sites with tall understories (1 m height) but is not palatable for many phytophages (Cooper-Driver, 1990). The negative association between phytophages and tall understories also might reflect that *P. aquilinum* prevents the development of other plants (Gliessman and Muller, 1978). Litter moisture content was the most influential individual predictor for ground decomposers and, to a lesser extent, for ground predators. Effects of moisture on decomposers were expected given the diet of these animals and their sensitivity to desiccation (e.g. isopods) (Paris, 1963; Purchart et al., 2013). The positive association of litter moisture with ground predators probably indicated the moisture requirements of prey; carabids often feed on earthworms and snails (Jelaska et al., 2014). Moreover, greater captures of predators at moist sites suggested that predators are promoted in mature woodlands. Old-growth forest stands often are moister and provide more resources to consumers than those younger (Schowalter, 1995; Siitonen et al., 2000), thereby enabling more predators (Duffy, 2003; Tews et al., 2004).

422   Although our study shows some clear associations between forest-patch

423   characteristics and arthropod assemblage composition and abundances, our conclusions

424   are from only 21 orders and 63 families of a highly diverse phyla in the Iberian

425   Peninsula with 115 families of dipterans alone (Carles-Tolrá, 2002). Our trophic guild

426   approach could be improved by using more advanced methods, such as trophic tracers

427   (e.g. nitrogen stable isotopes, McNabb et al., 2001; Thompson et al., 2005), given that

428   the exact trophic positions of captured arthropod taxa were uncertain. Moreover,

429   arthropods were sampled using pitfall traps, whose captures depend on arthropod

430   mobility, habitat structure, weather conditions, the number of traps used and content,

431   particularly bait traps (Melbourne, 1999; Sabu and Shiju, 2010; Manko et al., 2018).

432   However, the use of the same sampling design for the whole study area makes our

433   results comparable. The density of vegetation was unlikely to have much affected

434   ground traps because crawling arthropods were not only statistically associated with

435   understory height but were positively correlated with understory cover. Among the

436   captured flying insects, there were forest specialists (e.g. *P. pallida*) and 'wanderers'

437   (e.g. vespids, other flies), which may transfer microbes and affect ecological flows

438   among forests and other habitats, including rivers. Our results should be interpreted

439   such that the environmental conditions in the focal forests are suitable for the captured

440   flying insects if food is available. However, long-term data are necessary to understand

441   the complex dynamics of insects in general and of fermented-liquid feeders in

442   particular, including the relatively understudied dipterans.

443

5. Conclusions

445   The focal chestnut forest patches exemplified one of the major biodiversity

446   challenges in temperate regions, namely, the conservation of open old-growth

447   woodlands (Gondard et al., 2001; Lindenmayer et al., 2010; Miklín and Čížek, 2014;

448   Sebek et al., 2016). Given the high influence of surrounding habitats on open forests

449   (Murcia, 1995; Wright et al., 2010), chestnut woodlands are an exemplar to explore the

450   influence of streams in the complex dynamics of non-riparian arthropods. Effects of

451   stream distance on taxon richness and the abundance of arthropod guilds seemed to be

452   mediated mostly by vegetation structure. The exception was the strong association of

453   stream distance and the abundance of aerial predators, possibly because predators' home

454   ranges might include riparian habitats. Overall, various groups of arthropods were

455   positively associated with indicators of the presence of forest management (i.e. tall and

456 species-rich understories and low tree-species richness). Gains in the diversity and

457 abundance of arthropods with different food requirements might be had if the structural

458 development of vegetation is managed in a way that depends on stream distance.

459 Invertivores and ecosystem processes (e.g. nutrient cycling, pest control, pollination)

460 are likely to benefit from such a management strategy in chestnut woodlands and

461 systems of patches of other kinds of open temperate deciduous forests around the world.

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