PREPRINT

1 **Species-area relationships are modulated by trophic rank,**

2 **habitat affinity and dispersal ability**

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4 <u>**Authors:**</u> C.G.E. (Toos) van Noordwijk*[1,2,3], Wilco C.E.P. Verberk[1], Hans Turin[4],

5 Theodoor Heijerman[4,5], Kees Alders[4], Wouter Dekoninck[6], Karsten Hannig[7], Eugenie

6 Regan[8,9], Stephen McCormack[9], Mark J.F. Brown[8,10], Eva Remke[2], Henk Siepel[1,11],

7 Matty P. Berg[12,13] & Dries Bonte[3].

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9 [1] Department of Animal Ecology and Ecophysiology, Institute for Water and Wetland

10 Research, Radboud University Nijmegen, Heijendaelseweg 135, 6525 AJ Nijmegen, the

11 Netherlands

12 [2] Bargerveen foundation, Toernooiveld 1, 6525 ED Nijmegen, the Netherlands

13 [3] Department of Biology, Terrestrial Ecology Unit, Ghent University, K. L.

14 Ledeganckstraat 35, B-9000 Ghent, Belgium

15 [4] Loopkeverstichting (SFOC), Esdoorndreef 29, 6871 LK Renkum, the Netherlands.

16 [5] Biosystematics Group, Wageningen University, Generaal Foulkesweg 37, 6703 BL

17 Wageningen, The Netherlands

18 [6] Royal Belgian Institute of Natural Sciences, Vautierstraat 29, B-1000 Brussels, Belgium

19 [7] Bismarckstrasse 5, 45731 Waltrop, Germany

20 [8] Department of Zoology, Trinity College Dublin, Dublin 2, Ireland

21 [9] United Nations Environment Programme World Conservation Monitoring Centre, 219

22 Huntingdon Road,Cambridge,CB3 0DL, England

23   [10] School of Biological Sciences, Royal Holloway University of London, Egham, TW20

24   0EX, United Kingdom

25   [11] Nature Conservation and Plant ecology group, Wageningen University, P.O. Box 47,

26   6700 AA Wageningen, the Netherlands.

27   [12] Department of Ecological Science, VU University, Amsterdam, De Boelelaan 1085,

28   1081 HV Amsterdam, the Netherlands.

29   [13] Centre for Ecological and Evolutionary Studies, Community and Conservation Ecology

30   group, Postbox 11103, 9700 CC Groningen, The Netherlands

31   * Corresponding author: toos.vannoordwijk@gmail.com

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34   ABSTRACT

35   In the face of ongoing habitat fragmentation, species-area relationships (SARs) have

36   gained renewed interest and are increasingly used to set conservation priorities. An

37   important question is how large habitat areas need to be to optimize biodiversity

38   conservation. The relationship between area and species richness is explained by

39   colonization-extinction dynamics, whereby smaller sites harbour smaller populations,

40   which are more prone to extinction than the larger populations sustained by larger sites.

41   These colonization-extinction dynamics are predicted to vary with trophic rank, habitat

42   affinity and dispersal ability of the species. However, empirical evidence for the effect of

43   these species characteristics on SARs remains inconclusive.

44   In this study we used carabid beetle data from 58 calcareous grassland sites to

45   investigate how calcareous grassland area affects species richness and activity density for

46 species differing in trophic rank, habitat affinity and dispersal ability. In addition, we

47 investigated how SARs are affected by the availability of additional calcareous grassland

48 in the surrounding landscape.

49 Our results demonstrate that beetle species richness and activity density increase

50 with calcareous grassland area for zoophagous species that are specialists for dry

51 grasslands and to a lesser extent for zoophagous habitat generalists. Phytophagous

52 species and zoophagous forest and wet grassland specialists were not affected by

53 calcareous grassland area. The dependence of species on large single sites increased with

54 decreasing dispersal ability for species already vulnerable to calcareous grassland area.

55 Additional calcareous grassland in the landscape had a positive effect on local species

56 richness of both dry grassland specialists and generalists, but this effect was restricted to

57 a few hundred meters.

58 Our results demonstrate that SARs are affected by trophic rank, habitat affinity

59 and dispersal ability. These species characteristics do not operate independently but

60 should be viewed in concert. In addition, species' responses depend on the landscape

61 context. Our study suggests that the impact of habitat area on trophic interactions may be

62 larger than previously anticipated. In small habitat fragments surrounded by a hostile

63 matrix, food chains may be strongly disrupted. This highlights the need to conserve

64 continuous calcareous grassland patches of at least several hectares in size.

65

66 KEYWORDS

67 biodiversity, body size, community, flight ability, food chain, food web cascade,

68 fragmentation, generalist, nature conservation, specialist, trait, trophic level.

69   INTRODUCTION

70   Species-area relationship (SAR) theory predicts that species richness increases with area

71   (Williams 1943, Preston 1960, MacArthur and Wilson 1967). There are two main

72   ecological mechanisms underlying this long-standing and rigorously tested ecological

73   theory, which are not mutually exclusive. First, large areas tend to contain a larger

74   diversity of environmental conditions and biotopes, which support a greater variety of

75   species (Williams 1964), because species differ in resource requirements and

76   environmental tolerance to abiotic conditions. This is called the "habitat-diversity

77   hypothesis". The second mechanism, termed the "area-*per se* hypothesis" is derived from

78   the extinction-colonization equilibrium underlying classical island biogeography theory

79   (MacArthur and Wilson 1967). Extinction rates increase with decreasing population size

80   (Hanski 1999, Henle et al. 2004) and population density generally increases or remains

81   constant with increasing area (Connor et al. 2000). This implies that small sites harbour

82   small populations, which are more prone to extinction than the large populations

83   sustained by large sites. SARs have recently received renewed interest in the light of

84   conservation ecology and are increasingly used to predict extinction rates of target

85   species for nature conservation (e.g. Hanski et al. 2013) and to prioritize conservation

86   efforts (e.g. Steffan-Dewenter and Tscharntke 2000). An important question in this

87   respect is how large habitat areas need to be to optimize biodiversity conservation.

88   The minimum area of habitat required to support a viable community relates to

89   the 'area-per se hypothesis', which predicts that SARs depend on species-specific

90   colonization-extinction dynamics. Extinction rates decrease with habitat area (MacArthur

91   and Wilson 1967), while colonization rates are predicted to decrease with habitat

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92   isolation (MacArthur and Wilson 1967). This implies that SARs are also affected by the

93   landscape context (Hanski 1999, Hanski et al. 2013). Additional habitat in the landscape

94   will increase metapopulation persistence and hence colonization chances (Hanski 1999).

95   Here it is worth noting that SAR theory was initially developed for real islands, where the

96   surrounding matrix (i.e. non-habitat landscape) is clearly inhospitable for all terrestrial

97   species. When applying these principles to 'islands' of a specific biotope (e.g. calcareous

98   grassland) surrounded by other land-use types (e.g. arable land) the role of the matrix

99   becomes more complex (Haila 2002, Shepherd and Brantley 2005). While the matrix may

100 be hostile and unsuitable for specialist species, which perceive their habitat as

101 fragmented, the landscape may provide continuous habitat for generalist species (Driscoll

102 et al. 2013). A species' habitat affinity is thus likely to alter its response to biotope area

103 and site isolation (De Vries et al. 1996, Davies et al. 2000, Swihart et al. 2003).

104   In addition to habitat affinity, which influences how species perceive the

105 landscape, there are a number of other factors that affect extinction-colonization

106 dynamics. Colonization rates increase with increasing dispersal ability (Den Boer 1990a,

107 Tscharntke et al. 2002a). Extinction rates are determined by several species

108 characteristics (Verberk et al. 2010), including body size (Damuth 1981, Blackburn 1993)

109 and trophic rank (Holt et al. 1999). Body size has repeatedly been identified as a trait that

110 negatively affects population density, but the cause of this pattern is debatable because

111 size is correlated to several other traits affecting population density, including trophic

112 rank (Tscharntke et al. 2002a, Henle et al. 2004). Trophic rank affects extinction rates

113 because species from higher trophic ranks (carnivores and parasites) generally have both

114 lower population densities (Henle et al. 2004, Verberk et al. 2010) and increased

115   population fluctuations (Holt et al. 1999, Tscharntke and Kruess 1999, Henle et al. 2004,

116   Van Nouhuys 2005). The rationale behind this is that less energy is transferred through

117   successive links in the food chain, causing predators to be less abundant than prey of

118   comparable body size and reproductive rate (Hutchinson 1959, Heino 2008). In addition,

119   populations of higher trophic rank are likely to exhibit stronger numerical fluctuations, as

120   fluctuations of food (or prey or host) sources are exacerbated as they cascade up the food

121   chain (Holt et al. 1999, Van Nouhuys 2005). Despite this theoretical underpinning,

122   empirical evidence for the effect of trophic rank on the SAR has been inconsistent (Van

123   Nouhuys 2005) and it has been suggested that increasing SAR slopes with increasing

124   trophic rank should be limited to food specialists (Steffan-Dewenter and Tscharntke

125   2002, Henle et al. 2004). A complicating factor is that most studies to date have been

126   carried out in plant-herbivore and host-parasite systems (Tscharntke et al. 2002b, Van

127   Nouhuys 2005), where the species belonging to different trophic ranks also differ in other

128   respects. In these cases differences in body size and dispersal ability between trophic

129   ranks, may alternatively explain observed patterns, rather than trophic rank per se.

130   In this study we aim to investigate first, how the area of a biotope affects species

131   richness of a single monophyletic taxon that includes species that differ in trophic rank,

132   dispersal ability and habitat affinity. Secondly, we investigate how SARs for this taxon are

133   affected by habitat isolation. We use carabid beetles as a focal group because their ecology

134   has been widely studied (Koivula 2011, Kotze et al. 2011) and they exhibit considerable

135   variation in trophic rank, dispersal ability and habitat affinity (Turin 2000). This provides a

136   unique opportunity to study the effect of trophic rank on SAR independent of major body-

137   plan constraints. We performed this study in calcareous grasslands because this habitat is of

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138   high conservation value (WallisDeVries et al. 2002) and has become highly fragmented

139   over the past century across Europe (Baldock et al. 1996, WallisDeVries et al. 2002). Using

140   a meta-analysis of datasets from northwestern Europe, we test the hypothesis that carabid

141   beetle species richness will increase with calcareous grassland area. As we expect that such

142   increases are caused by an increase in population viability (following the area-per se

143   hypothesis), we expect carabid beetle activity density to also increase. We hypothesize that

144   the minimum area required for viable populations increases with trophic level due to

145   decreased population density and stability. This should cause zoophagous species to

146   respond more strongly to biotope area than phytophagous species. We also predict that

147   flightless species will be restricted to larger sites than species possessing good flight ability

148   and that additional calcareous grassland in the surrounding landscape will positively affect

149   carabid beetle richness in accordance with metapopulation theory (Hanski 1999). Given the

150   differences between species in their perception of the landscape we hypothesize that all of

151   these patterns will be contingent upon the habitat affinity of a species. The above

152   predictions should only hold for dry grassland specialists, while habitat generalists and

153   typical species of wet grasslands and forests will not be affected by the area of calcareous

154   grassland.

155

156   METHODS

157   **Study system**

158   Calcareous grasslands in northwestern Europe have a distinct carabid beetle fauna,

159   consisting mainly of thermophylic species, which are restricted to nutrient-poor

160   grasslands with a relatively warm microclimate (Lindroth 1949). In addition, calcareous

7

161   grasslands are inhabited by eurytopic species, which may also occur in various arable and

162   grassland habitats (Turin 2000). Large parts of northwestern Europe have seen a sharp

163   decline in the area and quality of calcareous grassland over the past century (Baldock et

164   al. 1996, WallisDeVries et al. 2002). Remaining sites are mostly surrounded by arable

165   land, fertilized grasslands and woodland.

166

167   **<u>Carabid beetle data collection</u>**

168   We collected six datasets from four countries containing pitfall trap data of carabid

169   beetles from unimproved (unfertilized) calcareous grasslands (58 sites, see Appendix A

170   for details). Descriptions of the sampling regions and vegetation types of these datasets

171   are given in Willems (2001), Regan & Brown (in prep), Dufrêne (1990), Eckel (1988)

172   and Hannig et al. (2005). The exact trapping method differed between datasets, but was

173   consistent within each dataset (Table 1). For the analyses, all data were pooled for each

174   calcareous grassland site.

175

176   **<u>Species characteristics</u>**

177   For each species in our dataset we determined trophic rank, habitat affinity, dispersal

178   ability and mean body size from literature (see Appendix B). We only included those

179   traits and trait categories for which we had reliable data for each species in our dataset.

180   Habitat affinity was categorized following Turin (2000) and Desender et al. (2008) with

181   "dry grassland specialists" defined as all species mainly occurring in dry, nutrient poor

182   habitats including calcareous grasslands and heathlands, "wet/forest specialists" defined

183   as species mainly occurring in wet habitats and forests and "open habitat generalists"

184 defined as all species occurring in a wide range of open habitats, including agricultural

185 land. We distinguished three trophic groups based on Turin (2000) and Saska (2004,

186 2005): 1) species that are strictly phytophagous throughout their life cycle (referred to as

187 phytophagous), 2) species that are at least partly zoophagous throughout their life-cycle

188 (referred to as zoophagous) and 3) species which are phytophagous as adults, but

189 zoophagous as larvae (referred to as trophic rank shift). Omnivorous species were

190 grouped together with strictly zoophagous species because we had insufficient

191 information for several species to classify them as either strictly zoophagous or

192 omnivorous (see also Vanbergen et al. 2010). Moreover, most of the species generally

193 classified as being zoophagous also incidentally feed on fruits and other plant material

194 (Thiele 1977). Species that shift from carnivory to herbivory during their life-cycle were

195 defined as a separate group. To date, these species have generally been classified as

196 phytophagous species, because most studies only incorporate adult feeding habits (see

197 e.g. Ribera et al. (1999) and Vanbergen et al. (2010)). We separated these species from

198 the continuously phytophagous species because we suspect that the larva is the most

199 critical stage in the life cycle (Thiele 1977), which would cause these species to behave

200 more like zoophagous species in our analysis. Dispersal ability was classified based on a

201 combination of wing morphology, flight muscle development and flight records from

202 window traps, following Den Boer (1990b), Turin (2000) and Desender et al. (2008). We

203 distinguished three categories: poor dispersers (species incapable of active flight),

204 intermediate dispersers (species capable of flight but with few flight records or low

205 proportions of macropterous individuals) and good dispersers (species with a large

206 proportion of the population capable of active flight and regularly caught in window

207   traps). The final species characteristic included in our analysis was body size, measured

208   as the total body length in mm, which was derived from Turin (2000) and Desender et al.

209   (2008). For statistical analyses, body size was divided into three classes: small (1-6 mm),

210   medium (7-10 mm), and large (11-35 mm), representing similar numbers of species.

211

212   **GIS analysis**

213   We mapped each calcareous grassland site on aerial images in ArcGis 9.2 (ESRI Inc.,

214   Redlands, CA, USA). Where available we used high quality free web mapping services

215   (e.g. Bing maps and Google maps). For some of the Irish sites the quality of freely

216   available aerial photographs was insufficient, instead we used 1m resolution

217   orthophotography maps supplied by Ordnance Survey Ireland. On all maps, good quality

218   (i.e. nutrient poor, well managed) calcareous grassland could quite easily be distinguished

219   from other habitat types, including more nutrient-rich or abandoned grassland, due to

220   clear colour differences. Site boundaries were always checked by people with field

221   knowledge of the sites. In addition to the sampled sites, we mapped all good quality

222   calcareous grassland sites in a 1000m radius around the centre point of each sampling

223   site. For each site we calculated the area of calcareous grassland (m^2) within each

224   sampling site and the area of calcareous grassland within a 500m and 1000m radius of the

225   sampling site (excluding the sampling site itself). These spatial scales were chosen

226   because flightless individuals generally do not cover distances of more than a few

227   hundred metres in their lifetime (Den Boer 1970, Thiele 1977).

228

229   **Statistical analysis**

230   Generalized linear mixed models (GLMM) were used to analyse the data, with dataset as

231   a random variable to account for regional differences in carabid beetle assemblage and

232   differences in sampling intensity between datasets. All analyses were performed

233   separately for the three habitat affinity groups: dry grassland specialists, open habitat

234   generalists and wet grassland and forest specialists (see above). The Irish dataset

235   contained only three species classified as dry grassland specialists, one for each trophic

236   rank (seven individuals in total). Even when adapting habitat affinity criteria to Irish

237   standards only few species could be characterised as being typical for dry grasslands

238   (Anderson et al. 2000). This is most likely due to the wetter and cooler climate in Ireland

239   in combination with its impoverished island fauna (Good 2004). For this reason the Irish

240   dataset was excluded from the analysis for typical dry grassland specialists. For the

241   analyses of generalists and wet grassland and forest specialists, the Irish dataset did not

242   differ structurally from the mainland datasets and was hence included, after checking that

243   the difference in the number of included datasets between habitat affinity groups did not

244   affect the results. We could not construct a single model including all three species traits

245   (trophic rank, dispersal ability and body size) because some combinations of trait classes

246   were empty (e.g. there are no large phytophagous species or poorly dispersing

247   phytophagous species). Moreover, all three traits are partly interrelated (Turin 2000,

248   Desender et al. 2008). Instead, we constructed three separate models, demonstrating the

249   effect of each of these traits separately on the SAR. We did this for dry grassland

250   specialist beetles only, because this was the only habitat affinity group for which we

251   expected an effect of these traits. We then focussed primarily on the trait that produced

252   lowest *P*-values (trophic rank) for further analyses on all three habitat affinity groups, but

253   performed additional analyses to ensure that the effects found were not caused by

254   interrelated traits (see below). For trophic rank, models were constructed for two

255   response variables: species richness and activity density (counts of individuals, which are

256   affected by both a species' density and its activity pattern). Activity density data were

257   natural log transformed to reduce the effect of highly active species (Ribera et al. 2001,

258   Vanbergen et al. 2010). Both species richness and transformed activity density followed a

259   Poisson distribution. All habitat size parameters were natural log transformed, in

260   accordance with general species-area relationship theory (Connor and McCoy 1979). For

261   both response variables, seven models were constructed (intercept only, calcareous

262   grassland size and calcareous grassland size x trophic rank, the latter two with no

263   additional landscape parameter, with additional calcareous grassland at the 500m scale or

264   with additional calcareous grassland at the 1000m scale), using the lmer function in R

265   package lme4 (Bates et al. 2013). Models were fitted using the Laplace approximation

266   and optimizing the log-likelihood rather than the Restricted Maximum Likelihood

267   criterion, as this method is better suited when comparing models with varying fixed

268   effects. Because the random part of the seven models was identical, AIC scores could be

269   used to rank models. Model averaging over all models scoring within 15 AIC points of

270   the best model was used to obtain parameter estimates and significance values (Bolker et

271   al. 2009). To ensure that reported effects of trophic rank were indeed caused by this trait

272   and not by co-linearity between trophic rank and dispersal ability, we also established

273   whether trophic rank had an effect on SAR within the group of dry grassland carabid

274   beetles with medium and good dispersal ability. The number of medium and good

275   dispersers was equal across trophic ranks, eliminating the co-linearity encountered when

276   including poor dispersers, which were all zoophagous. To do this, we used a GLMM

277   analysis (calcareous grassland size x trophic rank) with identical specifications as

278   described above. Finally, we tested for an independent effect of flight ability, by

279   analyzing the effect of this trait within trophic rank categories. Because the number of

280   species for each dispersal group was rather low within some habitat affinity and trophic

281   rank categories, we could not use a similar GLMM test here. Instead, we tested whether

282   the range of calcareous grassland sizes in which species were found, differed between

283   dispersal ability groups, providing an indication of the area requirements of each group.

284   To do this, we used Levene's test (centred round the median rather than the mean of each

285   group, to account for slight deviations from a normal distribution), as we were interested

286   in the range of site sizes, rather than the mean size of sites in which species of each group

287   occurred.

288

289   RESULTS

290   **Species-area relationships**

291   The six datasets combined held records of 23,540 carabid beetles belonging to 141

292   species. Of these, 2,983 individuals (13%) and 48 species (34%) were classified as dry

293   grassland specialists. Preliminary analyses showed that both trophic rank and flight

294   ability, but not body size, significantly altered the SAR of dry grassland specialists

295   (Appendix C). Because trophic rank had the most significant effect on SAR, further

296   analyses focused primarily on this trait (but see below). A full analysis on all three habitat

297   affinity groups revealed that both species richness and activity density were best

298   explained by models including calcareous grassland size, trophic rank and a measure of

299   additional calcareous grassland in the landscape (Table 2 & Appendix D). Additional

300   calcareous grassland in the landscape significantly increased the local species richness for

301   both dry grassland specialists and open habitat generalists, but not for forest and wet-

302   grassland specialists (Table 3). This effect was most pronounced when only including

303   additional calcareous grassland within a 500m radius and was only marginally significant

304   when including all additional calcareous grassland within a 1000m radius. Activity

305   density of dry grassland specialists was not affected by additional calcareous grassland

306   nearby (Table 4). However, activity density of open habitat generalists increased with

307   additional calcareous grassland especially at the 500m scale.

308

309   **<u>Trophic rank</u>**

310   Trophic rank significantly affected species-area relationships, but only for dry grassland

311   specialists (almost so for generalist species) (Fig. 1, Table 3). Within the dry grassland

312   specialists, phytophagous species were less affected by calcareous grassland size than

313   zoophagous species (significant interaction: area * phytophagous). The SAR for species

314   which shift in trophic rank during their life-cycle did not differ from zoophagous species

315   (Fig. 1, Table 3). It should be noted however, that the number of species shifting in

316   trophic rank was limited (six species in total). Activity density was affected by trophic

317   rank in much the same way as species richness (Fig. 2, Table 4). An additional GLMM

318   revealed that there was also a significant effect of trophic rank on SAR within dry

319   grassland specialists with medium and good dispersal ability (Appendix E). This

320   demonstrates that the effect of trophic rank on SAR is not purely a reflection of the

321   greater number of flightless species among zoophagous carabid beetles. Based on our

14

322   model parameter estimates we calculated predicted total activity density of zoophagous

323   and phytophagous carabid beetles in small, medium and large calcareous grasslands. This

324   revealed that total activity density of zoophagous species increases sharply with

325   calcareous grassland area, while the activity density of phytophagous species shows a

326   slight decline (Table 5).

327

328   **<u>Dispersal ability</u>**

329   The range of occupied grassland sizes differed significantly between dispersal groups for

330   zoophagous dry grassland specialists (Levene's test; $F_{2,54} = 4.53$, $p = 0.015$), but not for

331   other trophic groups or for habitat generalists (Levene's test; $F < 0.50$, $p > 0.50$). Dry

332   grassland specialists with poor dispersal ability were only found in the largest sites, while

333   dry grassland specialists with good dispersal ability were found in the widest range of

334   sites (Fig. 3).

335

336

337   DISCUSSION

338   Our meta-analysis demonstrates that the increase in carabid beetle species richness and

339   activity density with increasing area depends on both habitat affinity and trophic rank of

340   the species. This is the first time the effect of trophic rank on SARs has been studied

341   within a single monophyletic group. Previous studies all used phylogenetically highly

342   divergent taxa such as plant-herbivore or host-parasite systems (Tscharntke et al. 2002b,

343   Van Nouhuys 2005). Our study thus demonstrates that the effect of trophic rank on SARs

344   extends beyond herbivores and parasites and is not confounded by other factors specific

345   for host-parasite and plant-herbivore systems. We also demonstrate that the dependence

346   of species on large single sites increases with decreasing dispersal ability. Moreover,

347   additional habitat in the surrounding landscape has a positive effect on local species

348   richness, but not on activity density.

349

350   Habitat affinity

351   It has repeatedly been shown that SAR theory, which was initially developed for real

352   islands, also applies to 'islands' of a specific biotope (e.g. calcareous grassland)

353   surrounded by other land-use types (Davies et al. 2000, Steffan-Dewenter and Tscharntke

354   2000, Hanski et al. 2013). However, in contrast to real islands, the matrix surrounding

355   biotope 'islands' may be suitable habitat for generalist species, making SARs less

356   applicable (Davies et al. 2000, Shepherd and Brantley 2005, Driscoll et al. 2013). In line

357   with this, we showed that carabid species richness only strongly increased with

358   calcareous grassland size for dry grassland specialists. This demonstrates the importance

359   of adopting an organism-centered understanding of landscapes and habitat patches

360 (Shepherd and Brantley 2005), for example by incorporating species' habitat affinity (see

361 also De Vries et al. 1996). However, a difficulty with using habitat affinity classes is that

362 habitat affinity cannot be measured independent of a species' environment (see Violle et

363 al. 2007). Habitat affinity scores are generally derived from distribution records and

364 therefore depend on the availability of records and on the structure of the landscape in

365 which they are recorded. Species may therefore seem to have a wider tolerance of habitat

366 conditions than they actually have, because they can occur both in semi-natural grassland

367 and on arable land, but only under specific circumstances. This seems to be the case for at

368 least some of the generalist species in our study, as generalist zoophagous carabid beetle

369 richness increased with calcareous grassland area. Apparently some of the species

370 classified as generalists and assumed to be capable of surviving in the mainly arable

371 matrix, were still more or less restricted to calcareous grassland. As long as the causal

372 mechanism underpinning a species' habitat affinity remains unknown, it will remain

373 difficult to make accurate predictions.

374

375 <u>Landscape context</u>

376 Additional calcareous grassland in the vicinity had a positive effect on species richness

377 for dry grassland specialists in our study, as would be expected from island biogeography

378 theory (MacArthur and Wilson 1967). Surprisingly, this effect was also found for habitat

379 generalists, indicating again, that the surrounding landscape matrix does not form suitable

380 habitat for all generalists. The spatial extent of the effect of additional calcareous

381 grassland was limited to a few hundred meters, demonstrated by the stronger effect of

382 additional calcareous grassland at the 500m compared to the 1000m scale. In addition, the

383   positive effect of additional calcareous grassland in the landscape proved to be much

384   weaker than the effect of increased area. Additional calcareous grassland in the landscape

385   only affected species richness but not activity-density of dry grassland specialists. This

386   indicates that the influx of individuals from these additional areas is too small to affect

387   local population densities, but high enough to offer increased recolonization chances after

388   local extinction, contributing to community resilience.

389

390   <u>Significance of species-area relationships</u>

391   The slope of SARs may vary with sampling intensity (Hill et al. 1994, Cam et al. 2002).

392   More intensive sampling gives a better estimate of the true species richness, especially in

393   species rich sites, giving rise to steeper SARs. Therefore, the differences in sampling

394   duration (between 55 and 730 days) and in the number of traps per site (between 10 and

395   20) between our datasets may have affected the SAR slopes we found (sampling intensity

396   was identical across sites within datasets). In our models, we accounted for any

397   differences between datasets by including dataset as a random variable. However, not all

398   variance attributed to dataset was caused by sampling intensity, as our datasets also

399   differed in other respects (e.g. geographic region, landscape context, regional species

400   pool, climate and sampling year). Because of this, it is difficult to estimate the exact

401   effect of sampling intensity on the differences in SAR slopes between datasets in our

402   study. An effect of sampling intensity is most likely in the Irish dataset, which had the

403   lowest sampling duration (55 days, compared to 185 or more days for each of the other

404   datasets). However, the Irish dataset also deviates most from the other datasets with

405   respect to landscape and climate and has the most restricted regional species pool,

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406   making it impossible to attribute differences in SAR to any of these factors in particular.

407   Overall, sites included in our study were sampled relatively intensively, considering that

408   many studies use sampling periods of around 28 days (see for example Mayr et al. (2007)

409   and Wamser et al. (2012)). Therefore, we expect that effects of sampling intensity on our

410   overall results are limited. This is corroborated by the fact that the SARs found in our

411   study are very similar in slope to those previously reported for other arthropods. The z-

412   value (slope of the SAR) we found for zoophagous dry grassland specialists (0.48) is

413   identical to the z-value reported by Tscharntke et al. (2002b) for monophagous butterflies

414   in a similar arable land-calcareous grassland landscape. A study conducted on real islands

415   reported a z-value of 0.36 for total carabid beetle richness (Nilsson et al. 1988). These

416   slopes are around ten times higher than those reported for birds, mammals and

417   amphibians in a global study by Storch et al. (2012). This most likely reflects the smaller

418   spatial scale at which arthropods operate compared to vertebrate taxa. Importantly, the

419   high z-values for arthropods imply that even small decreases in habitat size can have a

420   significant ecological impact, especially if groups of species are differentially affected.

421   Our analysis demonstrated such variable responses for species differing in trophic rank

422   and dispersal ability. We were able to demonstrate that both characteristics had an

423   independent effect, i.e. effects were not solely caused by co-linearity between dispersal

424   ability and trophic rank. Poor and good dispersers occurred in many different genera,

425   making it unlikely that observed patterns were solely due to phylogeny rather than

426   dispersal ability. Similarly, habitat affinity classes were generally unrelated to phylogeny,

427   with dry grassland specialists and habitat generalists found in most genera. Trophic rank

428   was more strongly related to phylogeny, with only *Amara* (Pterostichinae), *Harpalus* and

429   *Ophonus* species (Harpalinae) being phytophagous, although other genera within those

430   subfamilies belong to different trophic ranks. The species classified as zoophagous, are of

431   very diverse phylogenetic origin. Species with an ontogenetic shift in trophic rank, which

432   are phylogenetically closely related to fully phytophagous species, responded in the same

433   way as zoophagous species. These are strong indicators that the observed responses are

434   causally related to trophic rank, rather than to underlying phylogenetic constraints or

435   other traits associated with phylogeny.

436

437   <u>Trophic rank modulates SAR</u>

438   Our results clearly demonstrate that zoophagous carabid beetles respond more strongly to

439   calcareous grassland area than phytophagous species. Our results also indicate that

440   phytophagous species with zoophagous larvae respond in a similar way to zoophagous

441   species, rather than phytophagous species, to which group they are usually assigned (e.g.

442   Ribera et al. 1999, Vanbergen et al. 2010). However, the number of species shifting in

443   trophic rank during their life cycle is limited (six species in our dataset), so these results

444   should be interpreted with caution.

445   An effect of trophic rank on SAR was previously predicted (Holt et al. 1999) and

446   empirically demonstrated (Steffan-Dewenter and Tscharntke 2000, Van Nouhuys 2005).

447   However, these studies argued that the slope of SARs should only increase with trophic

448   rank for food specialists (e.g. specialist parasitoids or monophagous consumers) as

449   generalists can compensate for low availability of one food source by utilizing alternative

450   sources, hence showing less population fluctuation. Additionally, food generalists, being

451   able to utilize multiple food sources, are predicted to have higher population densities

452   (Brown 1984). In contrast, our results suggest that trophic rank *per se*, i.e. irrespective of

453   food specialization, affects the slope of SARs. The zoophagous carabid beetles, for which

454   we have found an increased dependence on calcareous grassland area, generally feed on a

455   wide array of prey species (Thiele 1977, Turin 2000) and are thus food generalists. A

456   wide range of food sources may be insufficient to buffer against adverse conditions when

457   all food sources fluctuate in a synchronized manner, e.g. as a response to drought or other

458   adverse weather conditions. Moreover, population densities, which affect extinction rates,

459   were previously found to be lower for zoophagous species than for phytophagous species

460   across a wide array of species with differing food specialization (Verberk et al. 2010).

461   Several previous studies (Holt et al. 1999, Steffan-Dewenter and Tscharntke 2000, 2002,

462   Van Nouhuys 2005) did not find strong SARs for higher trophic rank generalists, in

463   contrast to our results. In both parasitoids and butterflies, the two main groups previously

464   used to study effects of trophic rank on SAR, food specialism is, however, strongly

465   correlated to habitat specialisation and often also to dispersal power (Bink 1992, Van

466   Nouhuys 2005). Thus, the differences found between food generalists and specialists may

467   represent a different perception of the landscape (more continuous versus highly

468   fragmented), rather than a different area dependence arising from food specialisation.

469   If trophic rank *per se*, rather than food specialisation, affects SARs, the impact of

470   habitat size on trophic interactions may be larger than previously anticipated. This

471   conclusion resonates well with studies on the effects of forest fragmentation, which have

472   demonstrated that carnivores respond more strongly to forest fragmentation than lower

473   trophic ranks independent of food specialisation (Didham et al. 1998, Davies et al. 2000).

474   The distinction between food specialisation and habitat specialisation may seem trivial,

475 especially because they are frequently interrelated. However, several authors have

476 previously argued that keeping them separate is important to better understand large scale

477 patterns (Gaston et al. 1997, Verberk et al. 2010). Our results also suggest vital

478 repercussions for the importance of the landscape context. If only food specialists depend

479 on larger sites, the number of generalist predators in a small site would be independent of

480 the surrounding landscape. However, if the area dependence of species is governed by

481 habitat affinity, species richness and density of predators in small sites declines sharply

482 with decreasing suitability of the surrounding landscape. This creates potential for

483 strongly disrupted food chains in isolated habitat fragments surrounded by a hostile

484 matrix. This could, for example, lead to spill-over effects of phytophagous pest species

485 into agricultural land (Kruess and Tscharntke 1994, Tscharntke et al. 2005). This

486 potential is also illustrated by our calculation of the predicted total activity density of

487 zoophagous and phytophagous carabid beetles in calcareous grasslands of different sizes.

488 Although activity-density is not a measure of absolute density (Thiele 1977), it does

489 reflect the impact of a species group because it represent the encounter rate or 'effective'

490 abundance (Den Boer 1977). Our calculation thus demonstrates that predation pressure in

491 small sites can be greatly reduced, while no such reduction was found for phytophagous

492 species. This adds to recent concerns that habitat loss may lead to serious community

493 instability and potentially threatens ecosystem service provision (Spiesman and Inouye

494 2013).

495

496 <u>Dispersal ability</u>

497   Dispersal ability affects species' vulnerability to habitat isolation (Den Boer 1990a,

498   Wamser et al. 2012). We demonstrated that this also leads to a restriction of poor

499   dispersers to larger sites, at least for zoophagous, dry grassland species. This is in line

500   with previous studies by De Vries et al. (1996). Although dispersal ability is partly

501   correlated with body size in carabid beetles (all large species are flightless), we were able

502   to demonstrate that the effect found here is caused by flight ability itself, as we found no

503   significant effect of body size on SAR.

504

505   <u>Implications</u>

506   Our results demonstrate that the effect of calcareous grassland area on species richness of

507   carabid beetles is affected by trophic rank and habitat affinity (affecting local extinction

508   chances) in combination with dispersal ability (affecting recolonization rates).

509   Interestingly, recent reviews found insufficient or inconsistent proof for the importance of

510   all three of these species' characteristics for SAR (Henle et al. 2004, Van Nouhuys 2005).

511   This apparent discrepancy is caused by the fact that species characteristics do not operate

512   independently (Davies et al. 2004, Van Kleef et al. 2006, Verberk et al. 2013). For

513   example, traits related to recolonization rates (dispersal ability) only become important

514   for species exhibiting characteristics which increase their local extinction chances

515   (combination of zoophagous and habitat specialist). In addition, we found that the

516   landscape context modulates the effect of specific species characteristics. Additional

517   patches of calcareous grassland in the surrounding landscape can supplement the

518   biodiversity of a particular location, but only with species with good dispersal ability and

519   over short distances. The quality of the surrounding landscape will affect the extent to

520   which habitat generalists can inhabit the matrix and hence the extent to which they are

521   limited by the area of one biotope type. In a hostile landscape, habitat generalists would

522   be expected to encounter similar restrictions as habitat specialists, causing them to

523   respond in a similar way to site size.

524   Our results indicate that of all dry grassland specialists, zoophagous species are

525   disproportionally affected by habitat fragmentation. In the six datasets, spanning four

526   northwestern European countries, zoophagous dry grassland specialists with poor

527   dispersal ability were virtually absent from calcareous grasslands smaller than 5 ha.

528   Trophic interactions may thus be seriously disrupted in smaller sites, especially if they

529   are surrounded by a hostile matrix. This highlights the need to conserve calcareous

530   grassland patches of at least several hectares in size.

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718

719   **Supplemental Material**

720

721   **Appendix A:** Map of sampling sites across Europe and data selection method.

722   **Appendix B:** Table of all carabid beetle species in our dataset and their characteristics.

723   **Appendix C:** Output for GLMM analyses testing for effects of trophic rank, dispersal

724   ability and body size on SAR.

725   **Appendix D:** AIC scores for the generalized linear mixed models of activity density per

726   habitat preference group.

727   **Appendix E:** Output for GLMM analysis to test for separate effect of trophic rank within

728   medium/good dispersing species.

729

730

Table 1. Specifications of the datasets included in the analysis. 'Symbol' refers to the symbols used in the figures.

Nr	Country	Nr of sites	Nr of traps per site	Trap diameter	Season	Trapping duration (days)	Year	Method reference	Symbol
1	Germany	3	20	8.5 cm	Apr.-Oct.	200	2006	van Noordwijk et al. 2012	●
2	Netherlands	15	10	8.5 cm	Apr.-Oct.	200	1988	van Noordwijk et al. 2012	▲
3	Germany	4	10	8.5 cm	March-Oct.	220	1986 or 1987	Eckel 1988	+
4	Germany	4	15-20	9 cm	All year	730	1995 and 1996	Hannig et al. 2005	□
5	Ireland	19	10	7 & 9 cm	May-August	55	2006	E. Regan pers. com.	■
6	Belgium	13	10	8.5 cm	Apr.-Oct.	185	1986 or 1987	Dufrêne 1990	*

Table 2. AIC scores for the generalized linear mixed models of species richness per habitat preference group. Dataset was included as a random variable in all models. Models within 15 AIC points of the best model are given in bold.

Model	Dry grassland	Generalist	Forest & wet grassland
.	244.9	448.2	685.4
Area	238.2	449.4	687.1
Area + 500m	230.9	437.6	686.1
Area + 1000m	234.7	446.8	685.8
Area x trophic rank	**130.8**	**182.4**	**149.6**
Area x trophic rank + 500m	**123.1**	**170.5**	**148.5**
Area x trophic rank + 1000m	**127.5**	**179.9**	**148.3**

1   *Table 3. Model averages for the fixed effects parameters in the best three generalized linear*

2   *mixed models for species richness. Significant effects are marked: * p ≤ 0.05, ** p ≤ 0.01.*

Fixed effect	Estimate	Std. Error	z value	p
Dry grassland				
(Intercept)	-4.47185	1.27327	-3.510	0.001**
Area	0.48402	0.11654	4.153	<0.001**
Trophic rank shift	-0.47318	3.38273	-0.140	0.889
Phytophagous	4.46496	1.40646	3.174	0.002**
Area x Trophic rank shift	-0.16320	0.31918	-0.512	0.608
Area x Phytophagous	-0.39842	0.13283	-2.999	0.003**
Additional calc. grass. 500m	0.04914	0.01597	3.076	0.002**
Additional calc. grass. 1000m	0.03574	0.01578	2.265	0.023*
Generalist				
(Intercept)	0.75861	0.437154	1.747	0.120
Area	0.07929	0.038182	2.075	0.046*
Trophic rank shift	-1.41957	1.068687	-1.328	0.184
Phytophagous	0.26232	0.64351	0.4073	0.684
Area x Trophic rank shift	-0.06933	0.100987	-0.686	0.492
Area x Phytophagous	-0.11146	0.061102	-1.824	0.068
Additional calc. grass. 500m	0.03654	0.009807	3.726	<0.001**
Additional calc. grass. 1000m	0.02017	0.009572	2.107	0.035*
Forest & wet grassland				
(Intercept)	1.43105	0.403642	3.555	0.001**

Area	0.04255	0.03525	1.206	0.235
Trophic rank shift	-2.87945	1.467678	-1.962	0.050*
Phytophagous	-0.63522	0.837104	-0.759	0.448
Area x Trophic rank shift	-0.01780	0.137981	-0.129	0.897
Area x Phytophagous	-0.11725	0.080532	-1.456	0.145
Additional calc. grass. 500m	0.01727	0.009739	1.774	0.076
Additional calc. grass. 1000m	0.01738	0.009585	1.813	0.070

3

4

5   *Table 4. Model averages for the fixed effects parameters in the best three generalized linear*

6   *mixed models for activity density (natural log scale). Significant effects are marked: * p ≤ 0.05,*

7   ** **p ≤ 0.01.*

Fixed effect	Estimate	Std. Error	z value	p
Dry grassland				
(Intercept)	-4.17339	1.30855	-3.188	0.002**
Area	0.45206	0.12044	3.753	<0.001**
Trophic rank shift	-0.34450	2.84219	-0.121	0.904
Phytophagous	5.65831	1.41822	3.989	<0.001**
Area x Trophic rank shift	-0.12237	0.26767	-0.457	0.648
Area x Phytophagous	-0.49899	0.13455	-3.708	<0.001**
Additional calc. grass. 500m	0.02512	0.01551	1.620	0.105
Additional calc. grass. 1000m	0.02090	0.01543	1.354	0.176
Generalist				
(Intercept)	0.57947	0.47250	1.235	0.260
Area	0.07121	0.04156	1.712	0.096
Trophic rank shift	-0.48149	0.82524	-0.584	0.560
Phytophagous	0.47163	0.68359	0.690	0.490
Area x Trophic rank shift	-0.06701	0.07679	-0.873	0.383
Area x Phytophagous	-0.10815	0.06397	-1.690	0.091
Additional calc. grass. 500m	0.03359	0.01047	3.209	0.001**
Additional calc. grass. 1000m	0.02625	0.01027	2.557	0.011*
Forest & wet grassland				

(Intercept)	0.61987	0.49592	1.258	0.234
Area	0.07720	0.04367	1.767	0.082
Trophic rank shift	-1.10087	1.19834	-0.919	0.358
Phytophagous	0.20281	0.81556	0.249	0.804
Area x Trophic rank shift	-0.09551	0.11373	-0.840	0.401
Area x Phytophagous	-0.13254	0.07773	-1.705	0.088
Additional calc. grass. 500m	0.02071	0.01126	1.839	0.066
Additional calc. grass. 1000m	0.02402	0.01114	2.156	0.031*

8

9

10   *Table 5. Calculations of the total activity density of carabid beetles of different trophic ranks in*

11   *small (1ha.), medium (10 ha.) and large (100ha.) chalk grasslands,based on the parameter*

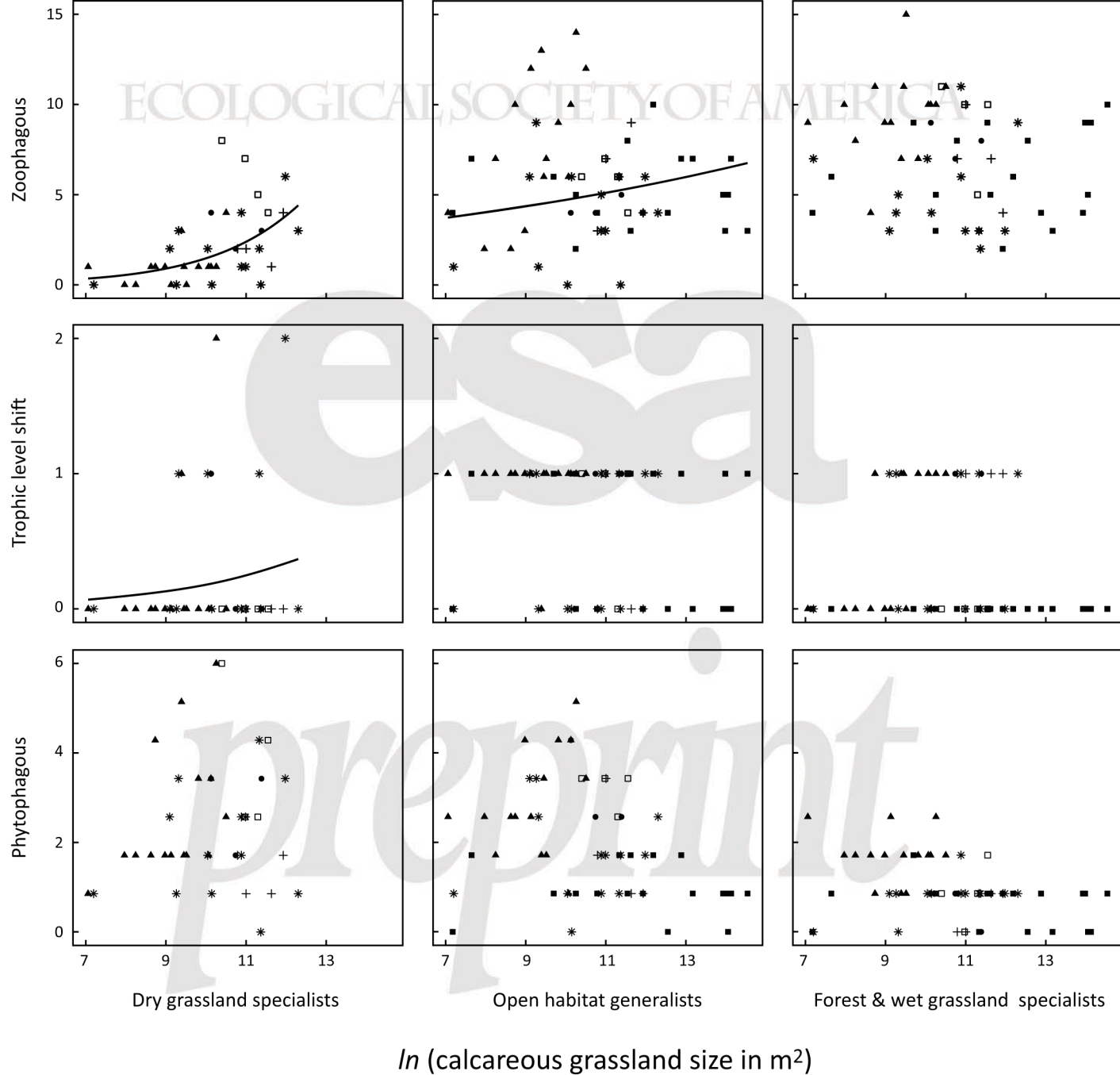12   *estimates derived from the GLMM analysis (see Table 3).*

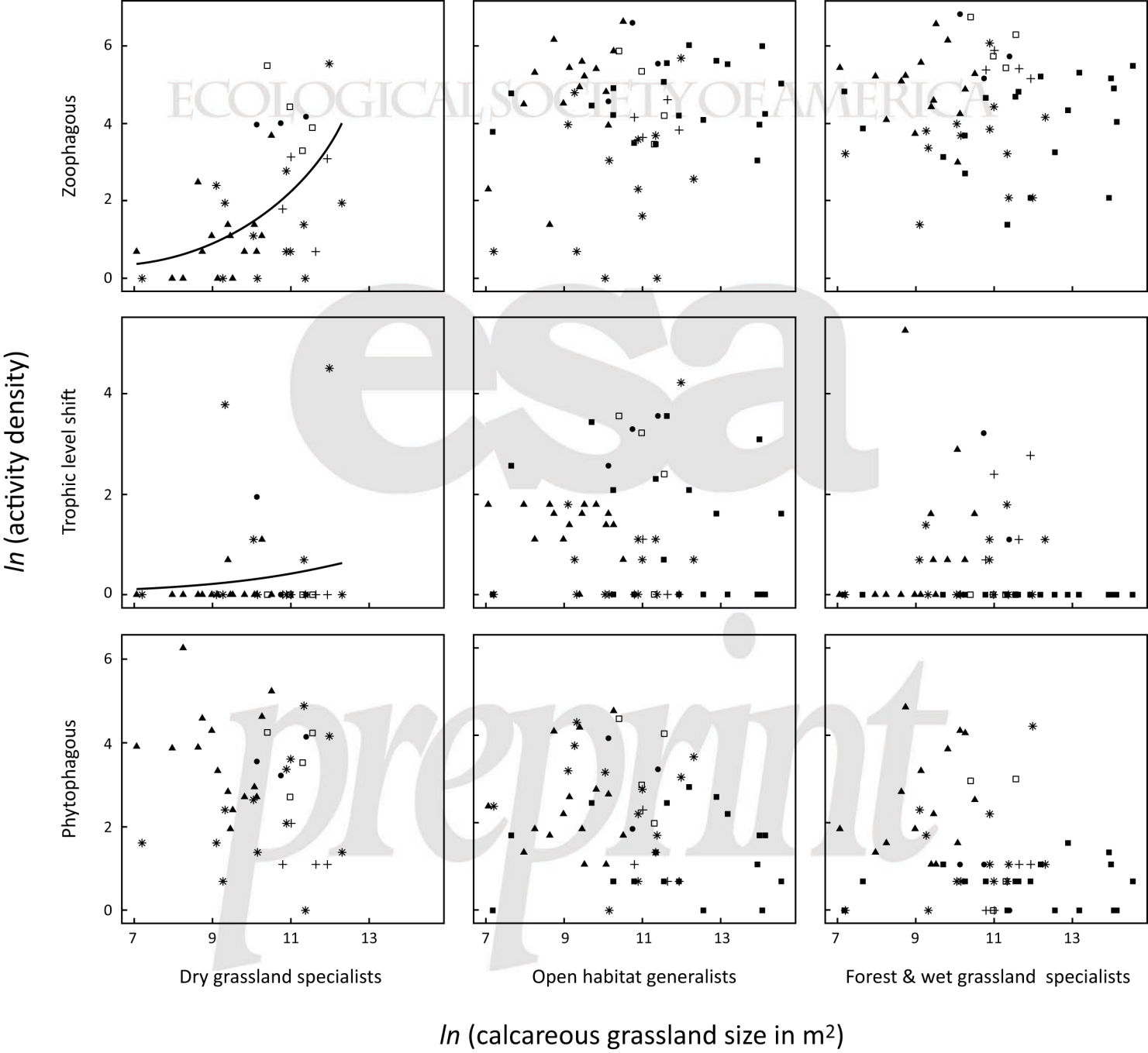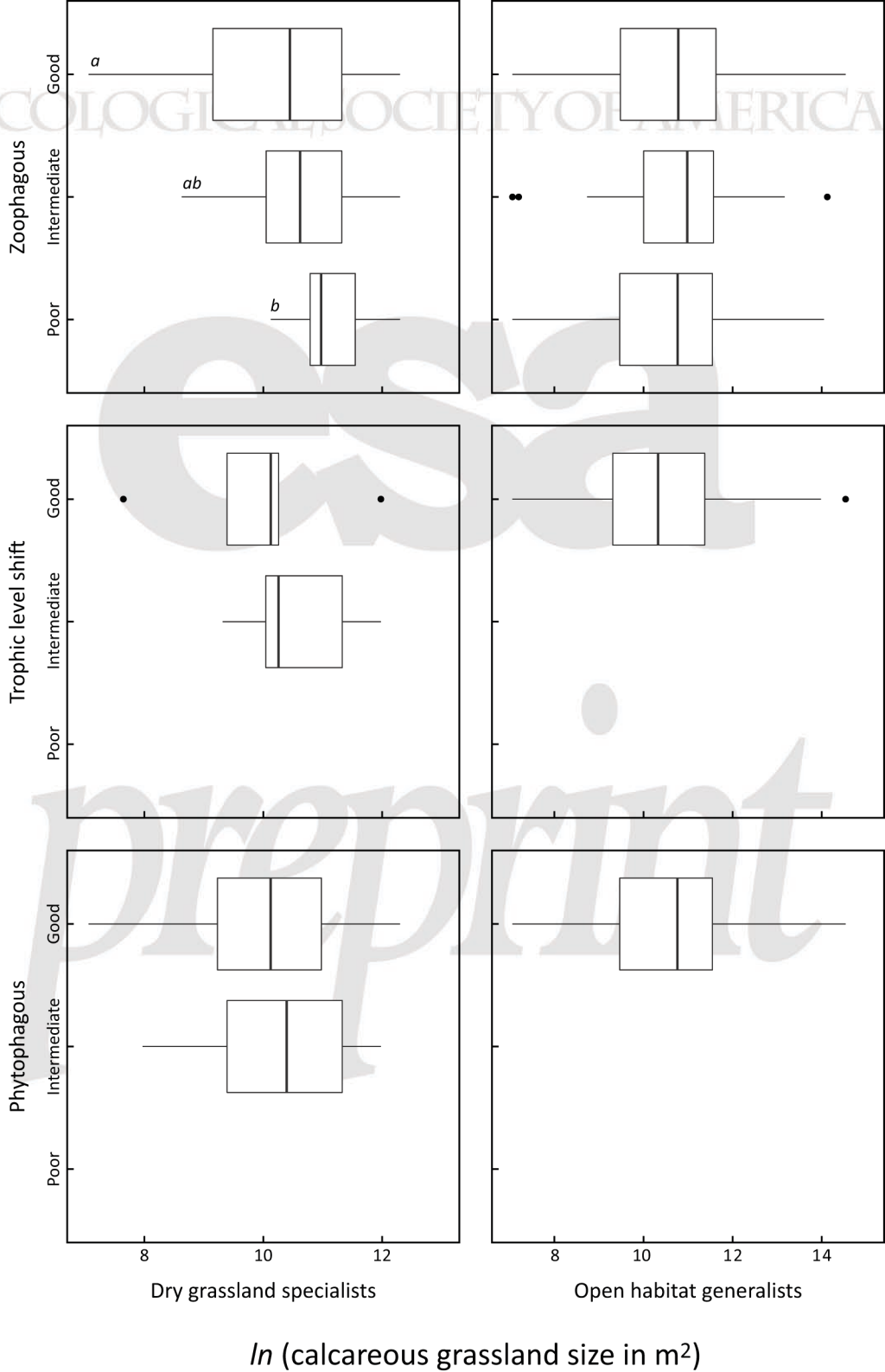| Site area →	1 ha.	10 ha.	100 ha.
Zoophagous			
Dry grassland	3	16	2309
Generalist	30	55	110
Forest & wet grassland	49	107	274
Total	**81**	**177**	**2693**
Phytophagous			
Dry grassland	16	12	9
Generalist	7	6	5
Forest & wet grassland	4	4	3
Total	**28**	**22**	**18**

13

14   *Fig. 1. Species richness of zoophagous species (upper panels), phytophagous species with*

15   *zoophagous larvae (middle panels) and phytophagous species (lower panels) as a function of*

16   *calcareous grassland size (natural log scale). Species are grouped by habitat affinity: typical dry*

17   *grassland species (left), generalist open habitat species (middle) and wet grassland and forest*

18   *species (right). Fitted lines (Poisson GLMM) are plotted where significant effects of calcareous*

19   *grassland size on species richness were found (see Table 2). Symbols represent different*

20   *datasets: ● = 1 Germany (2006); ▲ = 2 Netherlands (1988); + = 3 Germany (1986); □ = 4*

21   *Germany (1995); ■ = 5 Ireland (2006); * = 6 Belgium (1986).*

22

23   *Fig. 2. Activity density (natural log scale) of zoophagous species (upper panels), phytophagous*

24   *species with zoophagous larvae (middle panels) and phytophagous species (lower panels) as a*

25   *function of calcareous grassland size (natural log scale). Species are grouped by habitat affinity:*

26   *typical dry grassland species (left), generalist open habitat species (middle) and wet grassland*

27   *and forest species (right). Fitted lines (Poisson GLMM) are plotted where significant effects of*

28   *calcareous grassland size on activity density (natural log scale) were found (see table D1 in*

29   *Appendix D). Symbols represent different datasets: ● = 1 Germany (2006); ▲ = 2 Netherlands*

30   *(1988); + = 3 Germany (1986); □ = 4 Germany (1995); ■ = 5 Ireland (2006); * = 6 Belgium*

31   *(1986).*

32

33   *Fig. 3. Boxplots of occurrences of typical dry grassland (left) and generalist open habitat (right)*

34   *carabid beetles in calcareous grasslands of varying sizes by flight ability. Different letters*

35   *indicate significantly different variances of calcareous grassland size between flight ability*

36   *groups.*

Species richness

Zoophagous

Trophic level shift

Phytophagous

Dry grassland specialists

Open habitat generalists

Forest & wet grassland specialists

In (calcareous grassland size in m²)