

Dung Beetle Abundance, and Species Diversity, Are Maintained by Primates in Tropical Forest Fragments

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2 **FOREST FRAGMENTS.**
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14 **ABSTRACT:**

15 By processing quantities of dung to eat, dung beetles provide important services in forest ecosystems.
16 But, forest destruction and associated loss of mammals put these beetles at risk. Accordingly, we
17 evaluated the combined effects of forest area, edge effects and the abundance of mammals, on the
18 abundance and diversity of dung beetles in forest fragments using Structural Equation Modelling. We
19 aimed to contribute to the understanding of how changes in forest habitats influence these insects and
20 to the bigger concern about insects declines worldwide. Our study was located in forest fragments in
21 Tana River Kenya, where two endemic monkeys were the main source of dung.
22 Our optimal model explained a statistically significant 26% of the variance in the abundance of the
23 beetles, and 89% of the variance in their diversity. Forest area and abundance of mammals influenced
24 beetle abundance positively, but edge effects had a negative influence on the abundance. In turn,
25 beetle abundance influenced diversity directly and positively. Further, forest area and abundance of
26 mammals influenced beetle diversity positively, but these effects were indirect. Similarly, edge effects
27 influenced the diversity indirectly, but the effects were negative.

28 These findings imply that primates are crucial to maintaining the dung beetles in forest fragments
29 and the forests themselves because of the essential services beetles provide there. We recommend
30 that future studies investigate the factors, other than forest area, edge effects and the abundance of
31 mammals, which drive the abundance of the beetles.

32

33 **KEY WORDS:**

34 Africa; Conservation; Edge Effects; Habitat Fragmentation; Insect Apocalypse.

35 **INTRODUCTION:**

36 Insects are declining in abundance in many parts of the world (Vogel 2017; Wagner et al. 2021).
37 These declines are of serious concern because insects are integral to most food webs (Lister and Garcia
38 2018). Insects are food for a variety of other animals, and for many plants they provide essential
39 pollination services (Ollerton et al. 2011). Similarly, much cycling of nutrients in ecosystems is done by
40 insects which eat dead wood and animals, dung, foliage and fungi (Yang and Gratton 2014). Thus, the
41 loss of large numbers of insects from ecosystems can be disastrous.

42 Fortunately, it now appears that the insect declines may not be as geographically widespread as it
43 was first feared (Crossley et al. 2020), and that some groups of insects are unaffected (van Klink et al.
44 2020; Pilotto et al. 2020). Still, the apparent declines are a serious problem and every effort must be
45 made to understand what is really going on (Wagner et al. 2021). In so doing, the full scale of the
46 problem can be understood, and governments and society at large can address the problem
47 appropriately.

48 Many threats are driving the declines in the abundance and diversity of insects (Wagner et al.
49 2021). They are a constellation of threats, that are well known because they also drive the declines in
50 other taxa (Dirzo et al. 2014). These threats include habitat change, climate change, resource
51 overexploitation, invasive species and pollution of all sorts. Even so, perhaps the most serious one of all
52 these threats is habitat change (Oakleaf et al. 2015). Habitat change occurs when a natural habitat is
53 shredded by various factors, which reduces the area and disrupts the continuity. As a result and over
54 time then, what remains are many smaller patches isolated from each other by a matrix unlike the
55 native habitat. The associated reduction in area and increased isolation of the fragments then exposes
56 them to influences from the matrix and alters their microclimate, which impact the resident species in
57 various ways (Haddad et al. 2015).

58 Many studies have analyzed the effects of the changes in different types of habitats on a wide
59 variety of species, and there is no doubt that habitat change is indeed a serious threat to insects (Raven
60 and Wagner 2021). Accordingly, the goal of this study was to try to understand the ways in which
61 features of a fragmented forest habitat influenced the abundance and diversity of a charismatic group of
62 insects, the dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). To answer the question, how do
63 the amounts of forest habitat, abundance of mammals and edge effects (due to fragmentation) acting
64 together, influence the abundance and diversity of the beetles?

65 Dung beetles are essential in forest ecosystems because they process and bury large amounts of
66 dung. In doing so, they aerate the soil, cycle nutrients, disperse seeds and provide general sanitation
67 among many other services (Waterhouse 1974; Mittal 1993; Andresen and Levey 2004; Nervo et al.
68 2017). Even so, forest conversions are a serious threat to these beetles because forest clearing for
69 agricultural expansion is, perhaps, the most pervasive type of habitat change that there is (Foley et al.
70 2005). To make matters worse, dung beetles use the dung from mammals, almost exclusively, as food
71 at all stages of their development (Halffter and Edmonds 1982). So, to the extent that forest clearing
72 also diminishes the populations and species of mammals in the forests, it multiplies the threats to these
73 beetles (Culot et al. 2013; Raine et al. 2018).

74 One example of a forest habitat that has been fragmented, by a growing population of people in
75 need of land for agriculture is in the Tana River area of Kenya (Mbora and Meikle 2004; Mbora and
76 McPeck 2009). The forest is fragmented into patches of various shapes and sizes scattered across a
77 landscape in which, except for two species of endemic monkeys, are devoid of large mammals (Andrews
78 et al. 1975). The two species of monkey are forest dependent, constitute the majority of the biomass of
79 mammals in the forests and are, presumably, the main source of dung for the beetles there (David N. M.
80 Mbora, unpublished data). Therefore we chose this familiar, and well-studied, system to answer our
81 research question.

82 There are a number of ways in which the attributes of a fragmented forest habitat could influence
83 the abundance and diversity of the dung beetles (Fig. 1). And, three general ecological theories provide
84 appropriate frameworks within which to answer our research question. They are: the species area
85 relationship (Arrhenius 1921; Gleason 1922), the resource concentration hypothesis(Root 1973; Connor
86 et al. 2000) and the predictive model of edge response (Ries and Sisk 2004).

87 The species area relationship is the general pattern in which the total number of species increases
88 as the area from which they are sampled increases (Arrhenius 1921; Gleason 1922). The pattern exists
89 because as more and more individuals are collected from an increasingly larger area, then more and
90 more species are detected. In addition, the larger the area of a given locality then the more diverse the
91 habitats it can contain, and therefore carry many more species with different niches. Given the species
92 area relationship, we expected positive associations between the area of the forests, and the number of
93 species of the beetles. Synchronously, the area of the forests could affect the species richness of the
94 beetles indirectly, by its effects on the resident mammals. Certainly, the species area relationship works
95 on the species richness of the mammals too;- the larger the area of the forest the higher the species
96 richness of the mammals. Therefore, the larger the forests were, the greater the variety of dung types,
97 which would promote species richness of the beetles (Gittings and Giller 1998).

98 The resource concentration hypothesis posits that the population densities of animals are
99 correlated positively with the area of the habitats in which they are found (Connor et al. 2000). This
100 effect is especially pronounced, in highly fragmented landscapes (Andrén 1994). The effect can occur
101 due to any of several reasons, but two are pertinent for dung beetles in forest fragments. To start with,
102 beetles may be less likely to disperse as the area of habitat fragments increased (Risch 1981), which
103 would create a positive association between area and density of the beetles. Then, if the quality of the
104 habitats was associated with their areas, the populations of the beetles would tend to persist and
105 increase. Indeed, the number of monkeys and the area of forest fragments are strongly correlated in

106 these forests (Mborá and Meikle 2004; Wieczkowski 2004). Therefore, we surmised that the larger the
107 area of the forests was, the greater the number of the mammals that it would have (Andrén 1994;
108 Connor et al. 2000), which would in turn support a higher abundance, and species richness, of the
109 beetles (Andresen and Laurance 2007).

110 Finally, the predictive model of edge response (Ries and Sisk 2004) posits that the abundance and
111 species richness of organisms at the edge, are determined by the distribution of resources there. First, a
112 confluence of flows of energy and materials from either of adjoining fragments can build up resources at
113 the edge. Then organisms from either of the fragments can map onto these resources, now being much
114 more accessible to them. Given these postulates of the predictive model of edge response, we surmised
115 that edge effects would influence the abundance and species richness of the beetles in at least two
116 ways.

117 First, the microclimate of the edge could be quite unlike the interior of the fragments. Indeed,
118 forest edges adjoining open habitats are often hotter and drier than deeper in the forest (Chen et al.
119 1999). Such conditions are most favorable to species of beetles of the open habitat, but not so much for
120 the species adapted to the shaded interior of the forests. In this way, amounts of edge effects would
121 influence the abundance and species richness of the beetles by simultaneously favoring and disfavoring
122 some species. However, the magnitude and the direction of such effects are not easy to discern, *a*
123 *priori*. Secondly, the abundance of mammals, and therefore dung, at the edge can be quite different
124 than deep in the forest (Brodie et al. 2015). If some savanna mammals used edge habitats frequently,
125 then this could increase the abundance, and species richness, of the mammals as edge effects increased.
126 This greater abundance of mammals, and thus dung, at the edge would then promote the abundance
127 and species richness of the beetles;- as explained above for the species area and the resource
128 concentration effects. Conversely, as edge effects increased, it would reduce the quality of the forest

129 habitat for the monkeys, and their abundance too. Thus, as with the altered microclimates, the
130 magnitude and the direction of these effects are not be easy to discern.

131 To test the above postulates rigorously, we used Structural Equation Modelling, SEM for short
132 (Grace et al. 2010; Kline 2016). SEM is the proper tool here because it allows us to evaluate both the
133 direct and indirect effects in a straightforward way, as specified in the postulates (Fig. 1). What's more,
134 the testing of these postulates requires the use of covariates that cannot be observed and/or measured
135 directly. But with SEM these features can be analyzed as latent factors (Grace et al. 2010; Kline 2016).
136 Thus, SEM could yield insights into what direct or indirect processes drive the abundance and diversity
137 of the dung beetles in the forests. In so doing, it could then highlight processes that are important but
138 are otherwise unremarked, and point to areas in need of conservation intervention and/or further
139 studies.

140 **MATERIALS AND METHODS:**

141 MODEL SPECIFICATION

142 Following from the postulates (Fig. 1), we specified a starting latent Structural Regression (SR)
143 model with five factors, three exogenous and two endogenous (Fig. 2. The latent factor "Forest: spatial
144 attributes", encapsulates the ways in which the area of forest fragments could influence the beetles.
145 These ways include the species area effects on the beetles themselves, and the resident mammals which
146 provide the dung. In turn, the factor "Mammals: abundance & species richness", represents the
147 amounts and variety of dung found in the forests due to the abundance of mammals and their species
148 richness. And, the factor "Edge effects: microclimate & boundary", encapsulates the ways in which the
149 conditions and resources at the forest fragment edges could impact the dung beetles. The last two
150 latent factors represent the ways in which the dung beetles are influenced by the attributes of their
151 habitat as specified in the exogenous factors. The factor "Beetles: abundance", represents the
152 abundance in number of individuals or biomass of all the species of beetles. And, the latent factor

153 “Beetles: diversity”, encapsulates the combination of the number of different species and their relative
154 abundances. In this specification, species richness and diversity are not conceptualized separately. This
155 is because species richness and the other standard measures of diversity (Shannon and Simpson indices)
156 are really just special cases of one general equation (Roswell et al. 2021). Importantly, richness,
157 Shannon and Simpson can be denominated in the same units of species, and that is how we
158 conceptualized diversity (see below).

159 Commensurate with this model specification (Fig. 2), we then measured an array of attributes in
160 the field, to serve as potential reflective indicators for each of the latent factors. Majority of the
161 fieldwork was completed over June and July in 2009, 2010 and 2011.

162 DATA COLLECTION:

163 Study Area:

164 This study was located in a tropical forest remnant found along the Tana River in Kenya (Fig. 3). The
165 forest comprises 26 km² of fragments of various sizes (range, <1–220 ha), in a matrix of small-scale
166 farms and savannah shrubs (Mborá and McPeck 2009). Groundwater and occasional flooding maintain
167 the forest, restricting its lateral extent to about a kilometer on either side (Fig. S1a). It is a forest of high
168 conservation importance, because it supports a high diversity of rare plant and animal species (Andrews
169 et al. 1975). Particularly, the forest is the only known habitat of two endemic species of monkeys: the
170 Tana River red colobus (*Procolobus rufomitratu*s, Peters, 1879) and the Tana mangabey (*Cercocebus*
171 *galeritus*, Peters, 1879). The data reported here came from 12 forest fragments within the defunct Tana
172 River Primate National Reserve (TRPNR; Fig. 3). These study forests were a subset of forests that we had
173 used for earlier projects (Mborá and Meikle 2004; Mborá and McPeck 2009).

174

175

176

177 Forests Spatial Attributes, Abundance of Monkeys and of Forest Trees:

178 We determined the area (m²) and perimeter (m) of each fragment using QGIS (QGIS Development
179 Team 2019). Thus calculated their area-to-perimeter ratios and measured the centroid distance of each
180 forest to its edge.

181 Then, we surmised that the number of endemic monkeys in the fragments was a good measure of
182 the biomass of mammals in the forests. This is a reasonable assumption because these monkeys are
183 entirely forest dependent, and the fragments contain few other large mammals (David N. M. Mborá,
184 unpublished data). Thus, we adapted the monkeys census data from earlier projects (Mborá and Meikle
185 2004; Mborá and McPeck 2009) for use as the measure of abundance of mammals in the forests: the
186 numbers of individuals and of social groups for each species.

187 The abundance of the monkeys in the forests is associated positively with the abundance of trees,
188 but negatively with measures of forest use by people (Mborá and Meikle 2004; Wieczkowski 2004).
189 Therefore, we also measured the composition and abundance of forest trees, and the extent of forest
190 use by people, along transects as we had done previously (Mborá and Meikle 2004; Mborá and McPeck
191 2009). The forest tree data was then summarized per transect as basal area, (m²/ha) and density of
192 (individual trees/ha) of standing trees, and the trees that people had cut or otherwise damaged.

193 The Dung Beetles, Abundance and Diversity:

194 We sampled dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) along permanent transects
195 using standardized pitfall trapping (Larsen and Forsyth 2005). The number of beetle transects sampled
196 in each forest was proportional to the area of the forest, and in the same orientation as the vegetation
197 transects. Along each transect, sampling stations were established every 50 meters, from the riverbank
198 to the savanna edge of the forest, with one station set 50 meters into the matrix to characterize the
199 beetles of the transitional habitat at the edge (Fig. S1b).

200 Each sampling station was a quincunx of pitfalls in a five meter square. The trap was a plastic
201 screw-cap specimen jar, 236 ml, to which we added 100 ml of water mixed with an odorless detergent.
202 The traps were sunk into the ground with the rim at soil level, and as bait we dangled a 150g mass of
203 fresh cow dung wrapped in cheesecloth directly over the mouth of the trap. The whole set up was then
204 protected from rainfall by a plastic picnic plate held about 20 centimeters above the trap with yard
205 staples. The traps remained open in the field for 24 hours, after which we recovered and cleaned the
206 catch, separated the dung beetles from the other arthropods, and preserved everything in 70% ethanol.
207 Subsequently, we used taxonomic keys to identify the beetles to the level of species, or morphospecies,
208 and recorded the number of individuals of each species in each pitfall.

209 To estimate the biomass of each species in each pitfall, the average length of each species was
210 determined by taking two-point measurements from head to pygidium of 5 – 10 individuals with a
211 digital microscope (Keyence VHX, America). The average body length was then converted into a value of
212 body mass (Lobo 1993), and multiplied by the number of individuals of each species in each pitfall.

213 It is standard practice to classify dung beetles by one of three behavioral strategies;- dweller, roller
214 or tunneller. As well as by size; - small, medium and large. Therefore, we also classified the species in
215 each pitfall by the behavior with which they process dung and their body size, using guidelines from the
216 literature (Hanski and Cambefort 1991; Scholtz et al. 2008).

217 To optimize the data set, we pooled the five traps of a sampling station into a “sampling occasion”,
218 constituting one visit to one sampling station on one of the six sampling periods. Hereafter, the
219 “sampling occasions” are called plots. Then, we calculated the diversity of each plot as Hill numbers of
220 order $q = 0, 1$ and 2 using the iNEXT package version 2.0.19 in R (Hsieh et al. 2016). First, we calculated
221 the non-asymptotic diversity estimate of sample based rarefaction and extrapolation for the reference
222 sample, extrapolating to double. Then estimated the point diversity for each plot, for a sample coverage
223 of 95%. And finally, we estimated the asymptotic, or true, diversities of each plot.

224 To summarize for the beetles, we measured abundance, species richness and diversity for each
225 plot. Abundance was number of individuals and an estimate of their mass (milligrams), which was also
226 disaggregated by dung processing behaviors and body sizes for different species. Beetle diversity was
227 measured as Hill numbers in four different ways. In addition to these measures of diversity and
228 abundance, we also recorded the distance (meters) of each plot to the edge abutting the matrix, and to
229 the riverbank.

230 SELECTION OF FACTOR INDICATORS:

231 For each factor in the conceptual model (Fig. 2), there were multiple attributes that could have
232 possibly served as their reflective indicators. Therefore, we computed a correlogram of all attributes
233 (Fig. S2), and selected attributes as indicators for a given factor if their intercorrelations were positive,
234 and high in magnitude (Kline 2016). Given this criterion, the indicators of the starting, foundational,
235 SEM were as follows. Forest area emerged was the optimal indicator of the factor “Forest: spatial
236 attributes” *i.e.* a single indicator factor. The indicators of the factor “Edge effects: microclimate &
237 boundary” were: absolute distance of a plot to the matrix, the centroid distance of the fragment to the
238 matrix, and the perimeter of the forest. For the factor “Mammals: abundance & species richness”, the
239 indicators were: number of individuals of colobus and mangabey combined, number of groups of
240 colobus and mangabey combined, and number of individuals of mangabeys per forest. For the factor
241 “Beetles: abundance” the optimal indicators were, the mass of beetles disaggregated by behavior and
242 size (*i.e.* mass of tunneling, medium and large beetles). The factor “Beetles: diversity” the indicators
243 were, Hill.q0 and Hill.q1 for the reference sample, and asymptotic Hill.q0.

244 SEM theory requires that all data have a multivariate normal distribution. However, except for
245 Hill.q0, all the indicator variables were not normally distributed. Therefore, we transformed these non-
246 normally distributed attributes, as appropriate, to approximate normality.

247 FITTING AND ESTIMATION OF THE SEM:

248 In keeping with best practices of SEM, we implemented a two-step modeling (Kline 2016) in lavaan
249 version 0.6-6 using R (Rosseel et al. 2017). First, we specified the Structural Regression (SR) model as a
250 Confirmatory Factor Analyses model to ensure that the measurement part was consistent with the data.
251 Then, we fitted and estimated the fully latent SR model.

252 For purpose of models fitting, classical SEM theory assumes that all data are independently and
253 identically distributed (iid). However, the sampling framework of this study violates this iid assumption
254 because the plots were nested within forests, and the forest were also nested, east or west of the river
255 (Fig. 3; Fig. S1b). Therefore, to account for the sampling framework, the initial fit object from lavaan
256 was coded with an object specifying the sampling framework using lavaan.survey (Oberski 2014) to
257 estimate the fit of the final model. Then, we evaluated the adequacy of the final models as follows.

258 First for the global fit, we considered the fit statistics and three fit indices. A satisfactory model was
259 indicated by a non-significant χ^2 -statistic ($P > 0.05$). However, the alternative F reference distribution
260 was used also at the step where the sampling framework is specified in lavaan.survey ($P > 0.05$), because
261 the number of clusters was small (Oberski 2014). Further, a satisfactory model needed to attain specific
262 thresholds for three approximate fit indices as follows. A Comparative Fit Index, CFI > 0.90 ; Root Mean
263 Square Error of Approximation, RMSEA < 0.05 (for lower 90% confidence intervals); and a Standardized
264 Root Mean Square Residual, SRMR < 0.10 .

265 Second, we estimated the power of the final SR models (Preacher and Coffman 2006). We used the
266 tests of close-fit-hypothesis ($H_0: \varepsilon_0 \leq 0.05$, $H_1: \varepsilon_1 = 0.08$), and not-close-fit hypothesis ($H_0: \varepsilon_0 \geq 0.05$, $H_1: \varepsilon_1$
267 $= 0.01$) (Preacher and Coffman 2006).

268 Third, we assessed the significance of the individual factors in the final model using the
269 standardized path coefficients (β) and their P -values. Further, we used the path coefficients to calculate
270 the direct, indirect and total effects of the latent factors on the endogenous variables (Kline 2016). And,

271 the coefficients of determination (R^2) to assess how much of the variance of each endogenous variable
272 was due to the effects of the other variables.

273 **RESULTS:**

274 Our study forests, were located within 20 km of each other, and ranged in area from 8 to 220
275 hectares (Fig. S3). There were nine transects east of the river, in which we sampled 171 plots, and 12
276 transects from the west, where we sampled 117 plots (Fig. 3). Majority of the species sampled were
277 tunnellers (68 of 87, 78%), but their abundance was nearly equal to the rollers (Fig. 4). In terms of body
278 size, the majority were small or medium (80 of 87, 92%), and the diversity (Hill.q1 or Hill.q2) of all
279 beetles did not differ east and west of the river (Fig. S4).

280 The base model with five factors (Fig. 2) converged normally, and did not significantly deviate from
281 the data ($\chi^2 = 67.25$, $DF=56$, $P = 0.14$; Table S1). However, the solution was inadmissible due to
282 Heywood cases (Kline 2016), whereby the discriminant validity between the factors “Forest: spatial
283 attributes” and “Mammals: abundance and species richness”, was poor (covariance = 0.90, $SE = 0.014$;
284 Table S2; Table S3). Therefore, we trimmed the model to four factors in which we combined the spatial
285 and resources attributes into one factor “Forest and mammal abundance”, with indicators as forest
286 area, number of individuals of colobus and mangabeys combined, and number of individuals of
287 mangabeys. This re-specification was conceptually justifiable because the dimensional attributes of the
288 forests and the resident mammals must influence the abundance and diversity of the beetles
289 simultaneously. The other factors in the SR model, and their indicators, remained the same as specified
290 above.

291 The respecified model converged normally to an admissible solution, which did not significantly
292 deviate from the data ($\chi^2 = 72.33$, $DF=48$, $P = 0.44$; Table 1). This model explained most of the variance
293 (>65%) in nine of the 12 indicators of the four factors, demonstrating good convergent validity (Table 2),
294 and which was supported by the pattern of correlation residuals (Table S4; Fig. S5). Furthermore, four

295 of the six standardized factor correlations R^2 were well below 0.50 indicating reasonable discriminant
296 validity (Table 3).

297 Given $N = 288$, $DF = 48$, and $\alpha = 0.05$, the power for the test of the close-fit-hypothesis ($H_0: \varepsilon_0 \leq$
298 0.05 , $H_1: \varepsilon_1 = 0.08$), was 0.91, and that for the not-close-fit hypothesis, ($H_0: \varepsilon_0 \geq 0.05$, $H_1: \varepsilon_1 = 0.01$), was
299 0.83. Therefore, the probability of rejecting a false model, or detecting a correct one was good.

300 The standardized effect decompositions (Fig. 5; Table 4) revealed that the direct effects of forest
301 area and mammal abundance on edge effects were positive ($\beta = 0.89$, $SE=0.01$, $P = 0.00$; $R^2 = 0.75$), as
302 was on the dung beetle abundance ($\beta = 0.94$, $SE=0.11$, $P = 0.00$). However, the direct relationship
303 between edge effects and the abundance of dung beetles was negative ($\beta = -0.58$, $SE=0.08$, $P = 0.00$), as
304 were the indirect effects of the area and resource attributes on the abundance of dung beetles ($\beta = -$
305 0.51 , $SE = 0.08$, $P = 0.00$). Nevertheless, the total effects of forest area and mammal abundance on the
306 abundance of dung beetles were positive and statistically significant ($\beta = 0.43$, $SE = 0.04$, $P = 0.00$). The
307 model explained one quarter of the variance in dung beetle abundance ($R^2 = 0.26$).

308 The direct effects of the forest area and mammal abundance on the diversity of dung beetles was
309 negative, but not statistically significant ($\beta = -0.27$, $SE = 0.22$, $P = 0.23$; Fig. 5; Table 4). In contrast, the
310 indirect effects of the forest area and mammal abundance on the diversity of dung beetles were positive
311 and statistically significant ($\beta = 0.64$, $SE=0.26$, $P = 0.01$). Therefore, the total effects of the forest area
312 and mammal abundance on the diversity of dung beetles were positive and statistically significant ($\beta =$
313 0.37 , $SE=0.03$, $P = 0.00$; Table 4).

314 The direct relationship between edge effects and the diversity of dung beetles was positive but not
315 statistically significant ($\beta = 0.24$, $SE=0.20$, $P = 0.22$; Fig. 5; Table 4). However the indirect effects, of edge
316 effects on the diversity of dung beetles were negative and statistically significant ($\beta = -0.58$, $SE=0.14$, $P =$
317 0.00). Thus, the total edge effects on dung beetle diversity were negative and statistically significant (β
318 $= -0.33$, $SE=0.06$, $P = 0.00$). Ultimately, the direct effect of the abundance of the dung beetles on the

319 diversity of the beetles was strong and positive ($\beta = 0.99$, $SE=0.10$, $p = 0.00$). Overall our model
320 explained most of the variance in the diversity of the dung beetles ($R^2 = 0.89$).

321 **DISCUSSION:**

322 The finding that 92% of the dung beetle species were of a small or medium body size, suggests
323 strongly that the two endemic monkeys – the colobus and mangabeys – were indeed the primary source
324 of dung resources in the forests. The finding points to a general scarcity of dung, particularly large piles,
325 in the landscape because the larger the body of a mammal the more the dung that it produces
326 (Blueweiss et al. 1978). The two species of monkey are of medium body size and must produce small
327 volumes, and piles, of dung. Accordingly, the monkeys can only support beetles of modest body size
328 because the size of adult beetles is determined by the amount of dung available at the larval stage
329 (Moczek and Emlen 1999).

330 As we expected, forest area and mammal abundance were associated positively with the
331 abundance of dung beetles (Fig. 1 & 5; Table 4). This is as it should be because dung beetles use the
332 dung from mammals, almost exclusively, as food and to provision their larvae (Halffter and Edmonds
333 1982). Thus, this finding accords with the resource concentration hypothesis, which holds that as the
334 area of habitat fragments increases, then the abundance of animals increases also (Andr n 1994;
335 Connor et al. 2000). In the particular case of the Tana River forests, there is a strong correlation
336 between the number of monkeys and the area of forest fragments (Mborra and Meikle 2004), and
337 presumably dung resources. This also is consistent with studies from elsewhere showing positive
338 associations between the numbers of monkeys and the abundance of dung beetles in forests (Estrada et
339 al. 1999; Culot et al. 2013).

340 The relationship between the constructs Edge effects and Dung beetle abundance was negative and
341 statistically significant (Table 4; Fig. 5). This also is as expected because typically, as the area of a forest

342 fragment decreases, then its edge effects should increase, and the negative association is consistent
343 with the resource concentration hypothesis too (Connor et al. 2000).

344 Corresponding with the findings for beetle abundance, Forest area and mammal abundance had
345 positive effects on the diversity of the beetles, and the relationship of edge effects to the diversity of the
346 beetles was negative (Table 4; Fig. 5). However, this positive association is likely due to a combination
347 of the species area and the resource concentration effects. On one hand, the species area effect is a
348 foundational pattern (Arrhenius 1921), and on the other hand, resources determine the niche breadths
349 of the various species at a local scale (MacArthur 1972). Therefore, more species can be found in one
350 area than in another, if more resources are available, if each species overlaps broadly with its neighbors
351 in its resource usage, if each species is more specialized in its resource use, or if the resources dimension
352 is maximally exploited (MacArthur 1972). Thus, the more the dung resources there were in the
353 fragments, due to resource concentration (Connor et al. 2000), then the greater the species richness of
354 the beetles. Thus, the combined effects of the species area effect and resource concentration effect
355 should yield positive effects of the forest area and mammal abundance and the diversity of the beetles.

356 As well, the negative associations of the Edge effects and Dung beetle diversity are consistent with
357 the species area and the resource concentration hypotheses because the inverse relationships hold just
358 as well, but there is more. As the area of fragments decreased and so would the species richness and
359 the resource concentrations, but their edge effects would increase. However, the negative association
360 between the diversity and Edge effects can be due to other causes.

361 Generally, tunneling beetles build nests deeper in the soil than rolling beetles do (Halffter and
362 Edmonds 1982), which would protect their larvae from desiccation, and increased mortalities, due to
363 edge effects (Murcia 1995). Consequently, tunneling beetles tend to do better in forests with more
364 edge effects than rolling beetles (Nichols et al. 2013). Thus, edge effects and dung beetle diversity
365 associated negatively possibly because rolling beetles did not do so well, as edge effects increased.

366 Admittedly, this is not something we tested. However our data showed that the proportion of rollers
367 increased with the abundance of beetles (Fig. S6), and that the overall diversity was maximized at an
368 intermediate proportional mix of rollers (Fig. S7). Indeed, forests on the west bank which were
369 generally smaller in area (Fig. S3), tended to have more tunnellers than rollers (Fig. 4). A two-way
370 ANOVA of the number of beetles found a statistically significant interaction between behavior and side
371 of the river, $F(1, 1724) = 5.71, P = 0.02$. (Table S5; Fig. S8).

372 Our overarching aim in this study was to use SEM to analyze the joint effects of habitat variables on
373 the abundance and diversity of the dung beetles. We surmised that using SEM could provide insights
374 about the multiple processes operating in the system, uncover processes that may be operating but are
375 unrecognized, and point to areas needing further studies (Kline 2016). So then, what do the results tell
376 us about the processes operating in the system? What questions do they raise for further studies?

377 First, the findings tell us that primates in these forests are crucial to maintaining the abundance and
378 the diversity of the dung beetles. This is significant because it is, in all likelihood, true of tropical forest
379 fragments elsewhere. Many primates can thrive in forest fragments due to their flexibility of habitat
380 use, and are often the only resident large mammals. By supporting the dung beetles, the primates are
381 critical to maintaining the forests themselves because the beetles disperse seeds, speed up the cycling
382 of nutrients, and provide many other services in such habitats (Nervo et al. 2017).

383 Second, the direct effects on the diversity of dung beetles by the constructs forest area and
384 mammal abundance, and Edge effects were anomalous. While the effects of forest area and mammal
385 abundance on the diversity of the beetles were negative, those of edge effects were positive (Table 4;
386 Fig. 5). Both effects were not statistically significant, but they merit some examination as biologically
387 meaningful because they were contrary to our expectations, and findings from elsewhere (Klein 1989;
388 Feer and Hingrat 2005). Consistent with the findings for abundance, these effects imply that as the
389 forest area and mammal abundance decreased, (and edge effects increased) and so did the abundance

390 of dung beetles, but that somehow the diversity of the beetles increased. As it happened, the smaller
391 forests tended to have fewer monkeys (Fig. S3) but the two species were often sympatric in those
392 forests. Thus, it is possible that the opposite effects were due to the wider variety of dung types in
393 these smaller forests. If some of the beetles specialized on the dung of each monkey, then this could in
394 turn promote a higher species richness of dung beetles in the smaller forests.

395 There is another way the opposite effects could arise however. There was an apparent positive
396 association between proportional representation of rolling beetles and increasing forest area and
397 abundance of monkeys (Mбора et al. unpublished data; Fig. S6). This increasing proportion
398 representation of rolling beetles is consistent, to some extent, with the finding of a positive direct effect
399 of edge effects on diversity, but a negative association of edge effects with abundance (Table 4; Fig. 5).
400 This is so because increasing proportional representation of one behavior type necessarily corresponds
401 with reduced diversity (Fig. S7). Given this finding, one question begs to be answered, “in what ways do
402 the functional traits of the beetles influence how they respond to the habitat attributes”?

403 The use of functional traits to characterize communities in ecology is a growing and promising
404 approach (Brousseau et al. 2018). Functional traits are features of an organism that may influence its
405 performance and/or the ecological processes the said organism undertakes. Therefore, the approach
406 makes it possible to consider, at once, the capacity of an organism to survive and reproduce in a given
407 habitat, the outcomes of how it interacts with others, and the effects on the habitat. This approach can
408 allow to be discovered the factors that drive the species composition in the first place. Therefore, an
409 important avenue to follow up from our study is to analyze the ways in which the habitat variables
410 influenced the diversity and abundance of the beetles given their functional traits (Nichols et al. 2013).

411 Third, despite the statistically significant effects that we found, our model explained only 26% of
412 the variance in dung beetle abundance. Thus, most of the variance in the abundance of the beetles was
413 due to factors other than the ones we analyzed;- forest area, edge effects and the abundance of forest

414 mammals. Now, what factors could those be? We propose that the properties of the soil are one set of
415 factors that we did not measure, but which could greatly influence the abundance of the beetles
416 everywhere. After all, the dung beetles are soil fauna because larva and pupa stages constitute more
417 than 50% of the lifespan, during which they are confined within the soil (Halffter and Edmonds 1982).
418 So, to the extent that soil properties influence the viability of larvae and pupae, then they must
419 influence the abundance of the beetles overall. For example, sandy soils tend to support higher beetle
420 biomass, with rollers and tunnellers being equitably distributed, than clay soils which usually support
421 small rollers (Davis 1996). Even so, we are not aware of any studies on how changes in forest habitats
422 affect soil properties, and in turn communities of dung beetles. There is a need, therefore, for studies
423 that test rigorously the ways in which habitat changes influence soil properties, and in turn their effects
424 on the abundance and diversity of the soil insect fauna.

425

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441 **Consent to participate:** Not applicable.

442 **Consent for publication:** Not applicable.

443 **Availability of Data:** All relevant data produced from this study are provided in this manuscript and its

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445 <https://datadryad.org/stash/share/MROF5BuT74PifvaMAgEn5cWNAXM7TqS8Kj5prhYVhzk>

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TABLES:

Table 1: Global fit statistics of a two-step testing of the four factor structural regression model of the determinants of dung beetle abundance and diversity (* p-value from the F-reference distribution; ^aindicates retained model).

Model (N = 288)	χ^2	df	p	χ^2_D	df _D	p	RMSEA (90%CI)	CFI	SRMR
Measurement model, Abundance & Diversity:									
One factor – CFA	1269.95	54	0.00				0.28 (0.27 – 0.29)	0.54	0.21
Four factors – CFA	380.84	48	0.00	889.11	6	0.00	0.16 (0.14 – 0.17)	0.87	0.08
Four factors – CFA (ids=~east.west)	72.33	48	0.01 (*0.44)	308.51	0	0.00	0.04 (0.03 – 0.05)	0.97	0.07
Structural Regression model, Abundance & Diversity									
Three paths, unnested (ML)	380.84	48	0.00				0.16 (0.14 – 0.17)	0.87	0.074
▪ Nested (ids=~forest)	105.52	48	0.00 (*0.11)				0.07 (0.06 – 0.07)	0.81	0.074
▪ ^a Nested (ids=~east.west)	72.33	48	0.01 (*0.44)				0.04 (0.03 – 0.05)	0.97	0.074

Table 2: Robust maximum likelihood estimates of pattern coefficients and residuals of a four factor measurement model of the determinants of dung beetle abundance and diversity.

Factors and Indicators	Pattern Coefficients				Error Variances			
	Unstandardized		Standardized		Unstandardized		Standardized	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
A. Dung beetle abundance (mass, mg.)								
▪ Large body size	1.00	-	0.69	0.04	1.38	0.23	0.53	0.06
▪ Tunneling behavior	0.59	0.00	0.84	0.02	0.18	0.04	0.30	0.04
▪ Medium body size	0.47	0.00	0.813	0.03	0.14	0.04	0.34	0.04
B. Dung beetle diversity								
▪ Hill.q0	1.00	-	0.98	0.03	1.14	1.86	0.04	0.07
▪ Asymptotic Hill.q0	0.04	0.01	0.81	0.07	0.02	0.00	0.35	0.12
▪ Hill.q1	0.02	0.00	0.40	0.05	0.05	0.00	0.84	0.04
C. Forest area and mammal abundance								
▪ Forest area (m ²)	1.000	-	0.94	0.00	0.02	0.00	0.11	0.00
▪ Colobus & mangabey, individuals	0.92	0.06	0.94	0.02	0.01	0.00	0.11	0.04
▪ Mangabeys, individuals	0.86	0.23	0.82	0.07	0.04	0.04	0.32	0.12
D. Edge effects: microclimate & boundary								
• Absolute distance to matrix	1.000	-	0.49	0.01	0.17	0.02	0.76	0.01
• Centroid distance to matrix	18.45	0.24	0.60	0.07	33.30	12.96	0.64	0.08
• Forest perimeter	1.39	0.10	0.95	0.09	0.01	0.02	0.09	0.17

Table 3: Robust maximum likelihood estimates of factor variances and covariances for a four factor measurement model of the determinants of dung beetle abundance and diversity.

Parameter	Unstandardized		Standardized	
	Estimate	Standard Error	Estimate	Standard Error
Dung beetle abundance (DBA)	1.25	0.07	1.00	0.00
Dung beetle diversity (DBD)	26.20	0.89	1.00	0.00
Forest area and mammal abundance (FAMA)	0.12	0.02	1.00	0.00
Edge effects: microclimate & boundary (EE)	0.06	0.00	1.00	0.00
DBA ~~ DBD	5.37	0.37	0.94	0.05
DBA ~~FAMA	0.17	0.00	0.43	0.04
DBA ~~ EE	0.07	0.01	0.25	0.03
DBD ~~ FAMA	0.66	0.02	0.37	0.03
DBD ~~ EE	0.31	0.05	0.26	0.05
FAMA ~~ EE	0.07	0.01	0.89	0.01

Table 4: Standardized effect decompositions (standard errors) of the structural component of the structural regression model of the effects of Forest and mammal abundance, and edge effects, on dung beetle abundance and diversity (see Fig. 5).

Endogenous Factor	Effect	Forest area and mammal abundance	Edge Effects	Dung Beetle Abundance
Edge effects	Direct	0.89 (0.01)		
	Total indirect	-		
	Total	0.89 (0.01)		
Dung beetle Abundance	Direct	0.94 (0.11)	-0.58 (0.08)	
	Total indirect	-0.51 (0.08)		
	Total	0.43 (0.04)		
Dung beetle diversity	Direct	-0.27 (0.22) ^{NS}	0.24 (0.20) ^{NS}	0.99 (0.10)
	Total indirect	0.64 (0.26)	-0.58 (0.14)	
	Total	0.37 (0.03)	-0.33 (0.06)	0.99 (0.10)

FIGURE LEGENDS:

Figure 1: Conceptual meta-model of postulates of the ways in which attributes of the forest habitat could influence the abundance, species richness and diversity of the dung beetles. The amount of forest habitat could influence the abundance and species richness of the beetles in direct and positive ways. Simultaneously, the dimensional features of the fragments could influence the abundance and species richness of the beetles, indirectly through their effects on the resident mammals and edge effects. Lines with a single arrowhead represent hypothesized positive directional causal effects, except where indicated as unforeseeable (+/-), and could be positive or negative (see text for details).

Figure 2: The starting, foundational, structural component of the structural regression model of the effects of habitat attributes on dung beetle abundance and diversity, in compact symbolism. The single inward-pointing arrow represents exogenous variances and endogenous disturbances. Lines with a single arrowhead represent hypothesized directional positive causal effects, except where indicated as (+/-), which could be positive or negative (see text for details). Solid lines represent are the postulated main causal effects.

Figure 3: Map of the study area, showing distribution of the forests along the Tana River in Kenya, (TRPNR stands for Tana River Primate National Reserve).

Figure 4: The number of dung beetles (95% CI) found per plot east and west of the Tana River, classified by nesting behavior and body size. Most of the beetles were of a small body size.

Figure 5: The structural component of the structural regression model of the effects of habitat attributes on dung beetle abundance and diversity, with disturbances presented in compact symbolism. The top row are unstandardized estimates (Standard Error) and the bottom row are standardized estimates (Standard Error), from a completely standardized solution. All estimates are statistically significant (0.05 level) except where indicated "NS" (not significant).

FIGURES:

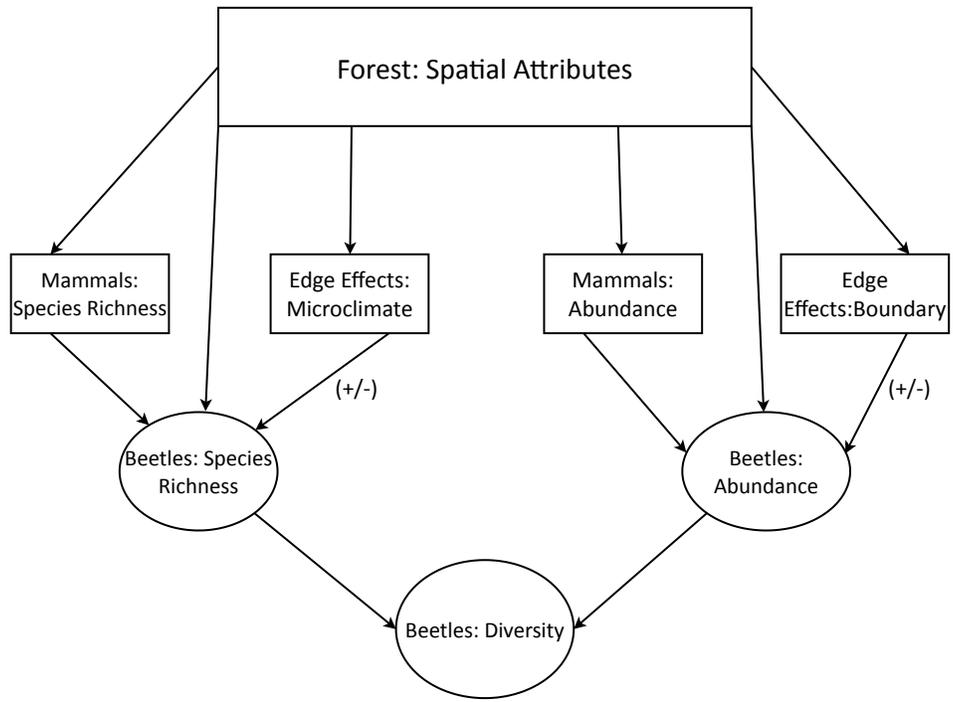


Figure 1:

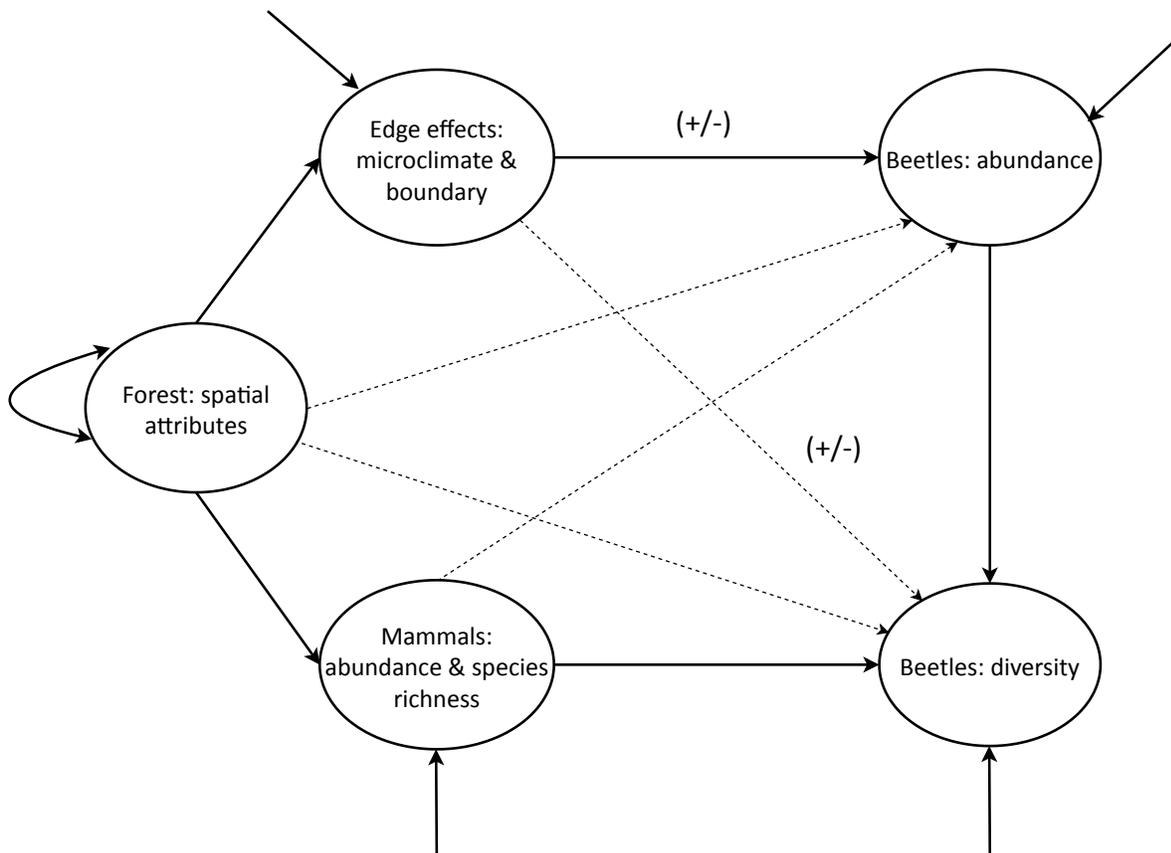


Figure 2:

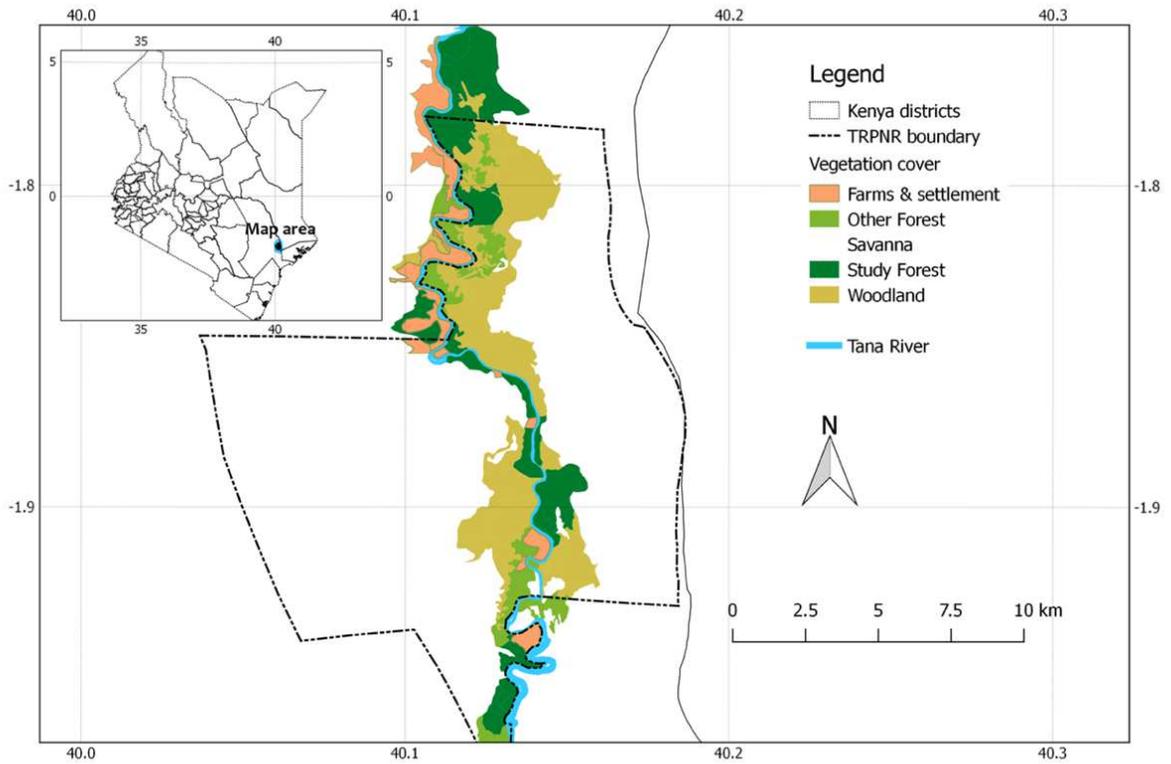


Figure 3:

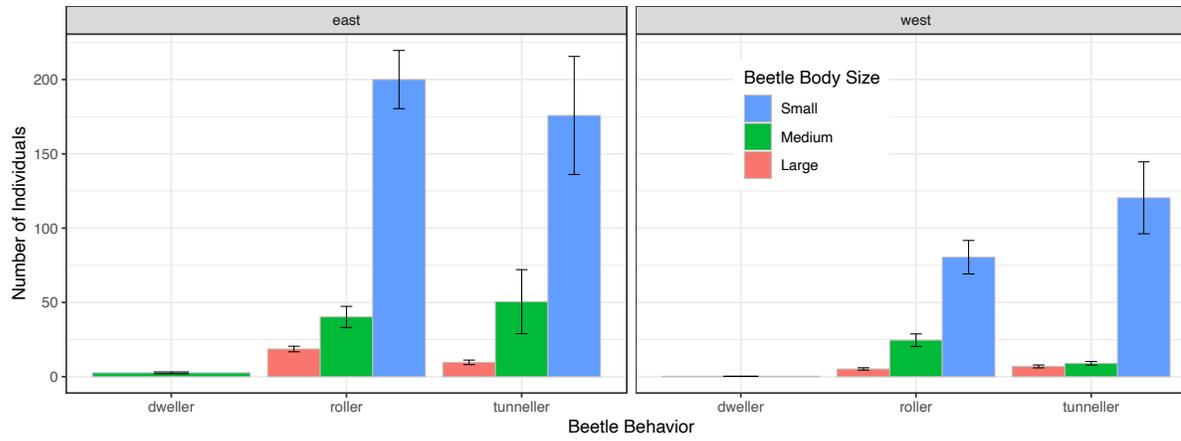


Figure 4:

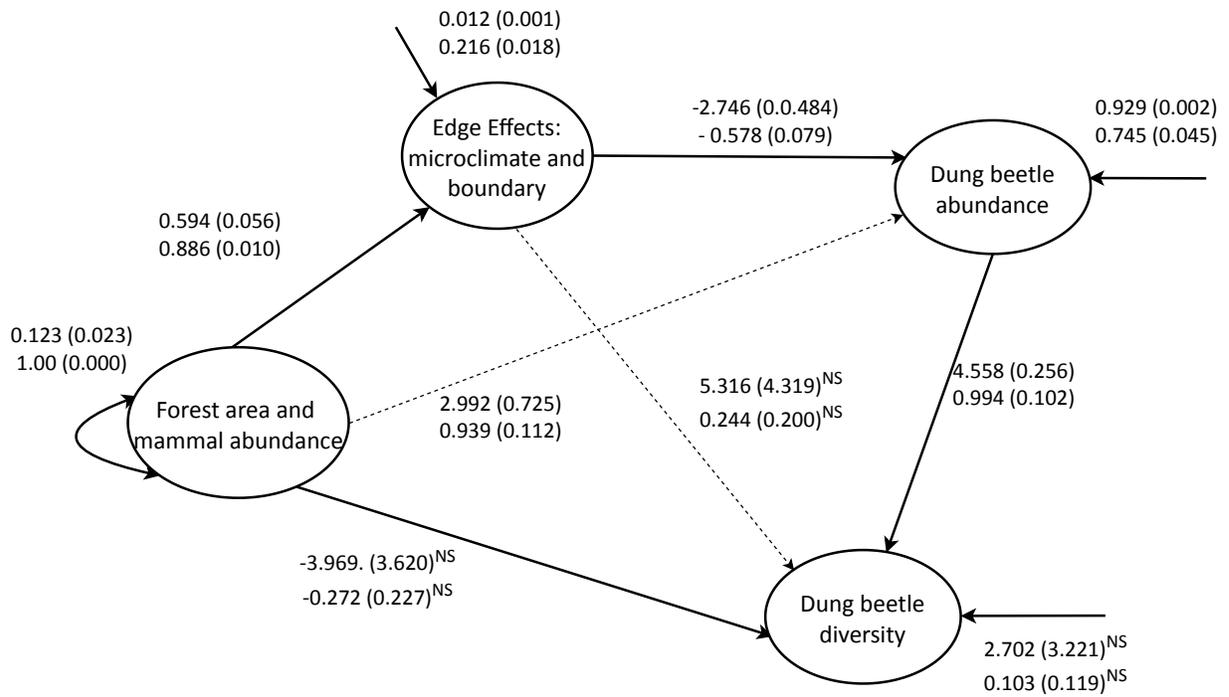


Figure 5: