Mechanisms of diversity maintenance in dung beetle assemblages in a heterogeneous tropical landscape

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Background. Anthropized landscapes play a crucial role in biodiversity conservation, as they encompass about 90% of the remaining tropical forest. Effective conservation strategies require a deep understanding of how anthropic disturbances determine diversity patterns across these landscapes. Here, we evaluated how attributes and assembly mechanisms of dung beetle communities vary across the Selva El Ocote Biosphere Reserve (REBISO) landscape.

Methods. Community attributes (species diversity, abundance, and biomass) were assessed at the landscape scale, using spatial windows and vegetation classes. Windows were categorized as intact, variegated, or fragmented based on their percent cover of tropical forest. The vegetation classes analyzed were tropical forest, second-growth forest, and pastures.

Results. We collected 15,457 individuals and 55 species. Variegated windows, tropical forests, and second-growth forests showed the highest diversity values, while the lowest values were found in intact windows and pastures. Landscape fragmentation was positively and strongly related to dung beetle diversity and negatively related to their abundance; biomass was positively associated with forest cover. Beta diversity was the primary driver of the high dung beetle diversity in the landscape analyzed.

Discussion. The landscape heterogeneity and its biodiversity-friendly matrix facilitate the complementarity of dung beetle assemblages in the Selva El Ocote Biosphere Reserve. Random processes govern beta diversity patterns in intact and variegated windows. Therefore, vegetation cover in the region is sufficient to maintain a continuous flow of dung beetles between forested landscape segments. However, intense anthropic disturbances acted as deterministic environmental filters in fragmented windows and pastures sites, leading to biotic homogenization processes. Our results suggest that increasing habitat variegation in highly fragmented sites is an effective strategy to prevent or buffer homogenization processes in the REBISO landscape.

1 **Mechanisms of Diversity Maintenance in Dung Beetle Assemblages in a**
2 **Heterogeneous Tropical Landscape**

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21 **Abstract**

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24 encompass about 90% of the remaining tropical forest. Effective conservation strategies require a
25 deep understanding of how anthropic disturbances determine diversity patterns across these
26 landscapes. Here, we evaluated how attributes and assembly mechanisms of dung beetle
27 communities vary across the Selva El Ocote Biosphere Reserve (REBISO) landscape.
28 **Methods.** Community attributes (species diversity, abundance, and biomass) were assessed at
29 the landscape scale, using spatial windows and vegetation classes. Windows were categorized as
30 intact, variegated, or fragmented based on their percent cover of tropical forest. The vegetation
31 classes analyzed were tropical forest, second-growth forest, and pastures.
32 **Results.** We collected 15,457 individuals and 55 species. Variegated windows, tropical forests,
33 and second-growth forests showed the highest diversity values, while the lowest values were
34 found in intact windows and pastures. Landscape fragmentation was positively and strongly
35 related to dung beetle diversity and negatively related to their abundance; biomass was positively
36 associated with forest cover. Beta diversity was the primary driver of the high dung beetle
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39 complementarity of dung beetle assemblages in the Selva El Ocote Biosphere Reserve. Random
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41 cover in the region is sufficient to maintain a continuous flow of dung beetles between forested
42 landscape segments. However, intense anthropic disturbances acted as deterministic
43 environmental filters in fragmented windows and pastures sites, leading to biotic homogenization
44 processes. Our results suggest that increasing habitat variegation in highly fragmented sites is an
45 effective strategy to prevent or buffer homogenization processes in the REBISO landscape.
46

47 **Introduction**

48

49 Anthropized neotropical landscapes encompass a complex combination of natural and semi-
50 natural habitats, where some species can thrive while others may go locally extinct (de Castro
51 Solar et al., 2015). Today, almost 90% of remaining tropical forests are located within
52 anthropized landscapes (Chazdon et al., 2009). These landscapes now play a crucial role in
53 biodiversity conservation agendas (DeClerck et al., 2010). Therefore, it is imperative to
54 understand how species diversity responds to anthropized landscapes in order to implement
55 suitable management actions (Gardner et al., 2009; Socolar et al., 2016), especially given the
56 multiple successional pathways and disturbance states that these modified landscapes can follow
57 (Fischer & Lindenmayer, 2007; Arroyo-Rodríguez et al., 2017).
58   Traditionally, researchers have assessed the effect of anthropic disturbance on biotic
59 communities by comparing one or more community attributes (e.g., species diversity, abundance,
60 biomass) across different sampling units at a local level (i.e., vegetation cover types or land-use

61 types). However, the composition and configuration of the habitats that surround the sampling
62 units are also important drivers of ecological processes in biotic communities (Franklin &
63 Lindenmayer, 2009). A landscape-level approach provides the necessary context to understand
64 better how communities respond to anthropic disturbances by incorporating the effects of the
65 multiple landscape components (Gardner et al., 2009; Hodder et al., 2014). Besides, landscape
66 studies provide useful information for effective natural resource management since many
67 anthropogenic drivers of biodiversity loss, e.g., land-use change or habitat destruction, operate at
68 the landscape level (Hodder et al., 2014).
69   McIntyre and Barret (1992) coined the variegation concept for anthropized landscapes
70 exhibiting disturbance and vegetation cover gradients. McIntyre and Hobbs (1999) then added
71 the fragmentation concept to the variegation model. These authors classified the landscape into
72 four categories based on the percentage of remaining original vegetation (OV) and the intensity
73 of habitat transformation: a) intact landscapes (>90% OV): sites with little or no modification; b)
74 variegated landscapes (60-90% OV), showing either gradual or abrupt limits between their
75 component units; c) fragmented landscapes (10-60% OV), characterized by a high degree of
76 modification; and d) relict landscapes (<10% OV), showing severe modification and almost no
77 forest cover remnants. Halffter and Rös (2013) proposed studying landscape diversity through
78 sampling windows in the geographical space analyzed. These windows are based on the
79 landscape model proposed by McIntyre and Hobbs (1992) and consist of equally-sized sampling
80 spaces that are semi-randomly located to maximize the representation of the vegetation
81 heterogeneity and land-use types in the landscape.
82   The Selva El Ocote Biosphere Reserve (REBISO, hereafter) harbors some of the most
83 heterogeneous, although highly disturbed, remnants of tropical forest in Mexico (Flamenco-
84 Sandoval, Martínez Ramos & Masera, 2007). Frequent forest fires, in addition to the complex
85 geological nature, climate features, and socio-economic dynamics (livestock and agricultural
86 activities) in the REBISO have led to a complex landscape comprising a mosaic of tropical
87 forests, second-growth forests, pastures, and croplands (Ochoa, 1996; SEMARNAT/CONANP,
88 2001; Flamenco-Sandoval, Martínez Ramos & Masera, 2007; Ramírez-Marcial et al., 2017).
89 Thus, a landscape-level approach seems most appropriate for examining how species respond to
90 anthropogenic disturbance in the REBISO, given its complex and heterogeneous landscape.
91   Dung beetles (Scarabaeidae: Scarabaeinae) are globally distributed insects that feed on
92 decomposing organic matter such as mammal feces, carrion, rotting fruit, or fungi (Halffter &
93 Matthews, 1966). Due to their sensitivity to environmental disturbances, dung beetles are ideal
94 bioindicators to assess the effects of landscape changes on diversity (Favila & Halffter, 1997;
95 Nichols et al., 2007). Previous studies have shown how habitat loss leads to abrupt changes in
96 the composition and structure of dung beetle communities (Klein, 1989; Quintero & Roslin,
97 2005; Nichols et al., 2007; Navarrete & Halffter, 2008; Díaz, Galante & Favila, 2010; Cajaiba et
98 al., 2017). However, few studies have evaluated the response of dung beetle communities to
99 disturbances at the landscape level (Numa et al., 2009; Rös, Escobar & Halffter, 2012; Sánchez-
100 de-Jesús et al., 2016; Alvarado et al., 2018, 2020), or whether the observed diversity patterns are

101   stochastic or determined by environmental filters or competitive exclusion between species
102   (Ortega-Martínez et al., 2020). Assessing dung beetle diversity at the landscape level, using
103   multiple but complementary metrics, can provide a more comprehensive view of how diversity is
104   maintained and what community assembly mechanisms operate in anthropized landscapes.
105   In this study, we evaluate the assemblage structure and diversity patterns of dung beetle
106   communities in the heterogeneous tropical landscape of the Selva El Ocote Biosphere Reserve.
107   We address the following questions: (1) How do the diversity and structure of dung beetle
108   assemblages vary across the REBISO landscape and its vegetation classes? (2) How do the
109   composition and configuration of the REBISO landscape influence the diversity and structure of
110   dung beetle assemblages? (3) How does beta diversity change and is maintained across the
111   landscape and between different vegetation classes? The information obtained in this study will
112   be useful for designing conservation strategies in complex tropical landscapes with different
113   heterogeneity levels.
114
115   **Materials & Methods**
116
117   **Study Area**
118
119   The study was carried out at the REBISO, located in the municipalities of Ocozocoautla de
120   Espinosa and Cintalapa, Chiapas, Mexico (16°45'42" - 17°09'00" N and 93°54'19" - 93°21'20"
121   W, Fig. 1). The area is mostly underlain by dolomite rocks and limestone, with a dominance of
122   water-soluble sedimentary rocks (Domenici, 2016). The predominant climate types are warm,
123   humid (climate type Am) and warm, subhumid (climate type Am(f)), with a mean annual
124   temperature of 22 °C and heavy rainfall throughout the year (SEMARNAT/CONANP, 2001).
125   We produced a vegetation map of REBISO from a multispectral SPOT6 image acquired
126   in 2014, using a supervised classification method in QGIS v2.12.3 (QGIS Development Team,
127   2016). The vegetation classes considered were tropical forest, second-growth forest, and pastures
128   (Fig. 1, Table 1).
129
130   **Sampling Design**
131
132   We established eight 1-km^2 (100 ha) sampling windows to capture the landscape heterogeneity
133   in the REBISO (Sánchez-de-Jesús et al., 2016). Each window was separated from each other by
134   at least 2 km to ensure spatial independence between them (Sánchez-de-Jesús et al., 2016). The
135   landscape composition in each window was described by estimating the percent coverage of each
136   vegetation class and evaluating the evenness of their distribution (landscape compositional
137   diversity - Shannon diversity). The spatial configuration of the vegetation classes in each
138   window was assessed with the splitting index and edge density metric (McGarigal, Cushman &
139   Ene, 2012). Edge density is computed as the length (m) of the edges of each vegetation class
140   divided by the window area (ha). The splitting index describes the degree of fragmentation of a
141   landscape and is equivalent to the effective number of patches. Thus, as a landscape becomes

142 increasingly sub-divided, the splitting index increases (Jaeger, 2000; Fahrig, 2017). The
143 landscape composition, edge density, and splitting index metrics (Table S1) were obtained with
144 FRAGSTAT v4.2.1 (McGarigal et al., 2012). Based on the percent cover of tropical forest (F),
145 windows were classified as intact (W1, W2; F > 90%), variegated (W3, W4, and W5; 60% < F <
146 90%), or fragmented (W6, W7, and W8; 10% < F < 60%).
147   We sampled dung beetles (Scarabaeidae: Scarabaeinae) during the dry (March to May)
148 and the rainy (July-August) seasons of 2016 using pitfall traps. This sampling scheme allowed us
149 to integrate the seasonal activities of dung beetles (Cajaiba et al., 2017). Each trap consisted of a
150 1 L cylindrical plastic container with 300 mL of ethylene glycol as preservative, buried at ground
151 level, and covered with a plastic lid to protect the bait from rain and sun radiation. Pitfall traps
152 were baited with 70 g of either an 80:20 mixture of pig and human feces (copro-traps) or squid
153 flesh (necro-traps) in order to obtain a representative sample of the dung beetle assemblages in
154 the area.
155   Seven sampling sites were established in each window, separated 250-360 meters from
156 each other, to proportionally adjust the number of pitfall traps per vegetation class according to
157 the vegetation class composition of each window (Table S2). Proportional sampling is a suitable
158 method for detecting changes in beta diversity in heterogeneous landscapes (Schoereder et al.,
159 2004). In each sampling site, three copro-traps and three necro-traps (42 traps/window), were
160 placed in a rectangular area separated 50 m from each other to minimize interference between
161 them (Larsen & Forsyth, 2005). The rectangular layout of some trap sets was modified in some
162 cases due to the topographic characteristics of the sites. The pitfall traps were left active for 48
163 hours.
164   The specimens collected were counted and identified to species. To estimate the dung
165 beetle biomass, we randomly selected ten specimens of each species and dried them at 70 °C for
166 72 hours. We weighed each specimen to the nearest 0.1mg with an analytical balance (Explorer
167 Pro) and calculated the average biomass for each species. Finally, we multiplied the mean
168 biomass of each species by its abundance in each window and vegetation class. The dung beetle
169 specimens were deposited in the entomological collection of El Colegio de la Frontera Sur, San
170 Cristóbal de Las Casas. Field sampling in the REBISO was carried out under permit
171 SGPA/DGS/14214/15 issued by the Secretaria de Medio Ambiente y Recursos Naturales,
172 Mexico.
173
174 **Data Analysis**
175
176 We followed a spatial and structural approach (*sensu* Rös, Escobar & Halffter, 2012) to analyze
177 the data. Windows were the sampling units for the spatial approach (n = 8), while vegetation
178 classes within windows were the sampling units for the structural approach (n = 21). The
179 sampling completeness of each window and vegetation class was determined using the coverage
180 estimator of Chao and Jost (2012), which allows comparing species diversity across multiple
181 sites.

182   Alpha diversity in each sampling unit (window or vegetation class) was evaluated using
183 the ^0D and ^1D diversity numbers. ^0D is equivalent to species richness and is insensitive to the
184 species abundance (Jost, 2006); ^1D is equivalent to the exponential of Shannon diversity index
185 and accounts for the most abundant species in a community (Jost, 2006).
186   We examined differences in species richness between windows by constructing and
187 comparing their 95% bootstrap confidence intervals. Non-overlapping confidence intervals
188 denote significantly different species richness (Gotelli & Colwell, 2011; Chao et al., 2014).
189 Differences in species richness between vegetation classes were determined using interpolation–
190 extrapolation curves (Chao et al., 2014). The sampling coverage, ^0D and ^1D diversity numbers,
191 confidence intervals, and the interpolation–extrapolation curves were obtained with the software
192 iNEXT v2.0.11 (Hsieh, Ma & Chao, 2016).
193   Generalized linear models (GLM) were used to assess differences in abundance and
194 biomass between windows and vegetation classes. The abundance and biomass data approached
195 a normal distribution after logarithmic transformation and were analyzed assuming a Gaussian
196 error distribution (Crawley, 2013). Pairwise comparisons using Tukey's test were carried out,
197 with the multcomp package (Hothorn et al., 2016) whenever significant differences were
198 detected.
199   GLMs were also used to assess the effect of the landscape composition and configuration
200 on the species richness (^0D), exponential of the Shannon diversity (^1D), abundance, and biomass
201 of the dung beetle assemblages. These data were first tested for normality and were then
202 analyzed assuming a Gaussian error distribution. Since only eight observations were available to
203 fit these models, separate models containing only one predictor variable were constructed to
204 avoid overfitting (Kelley & Maxwell, 2003). The best-fit models were selected based on the
205 Akaike′s information criterion corrected for small samples (AICc) and the deviance explained
206 (D^2). The model with the smallest AICc (ΔAICc >2) and the largest D^2 values was selected as the
207 best-fit model (Burnham & Anderson, 2002). Based on the results from the Moran I test (as
208 implemented in the package LetsR), no significant spatial structure was detected in the response
209 variables (Table S3) (Vilela & Villalobos, 2015).
210   True beta diversity (i.e., the effective number of distinct communities) was estimated for
211 species richness ($^0\beta$) and Shannon diversity ($^1\beta$) using the multiplicative partitioning method
212 (Jost, 2007). The multiple-site *Sørensen* dissimilarity was partitioned as $\beta_{Sor} = \beta_{Sim} + \beta_{Sne}$ using
213 the package Betapart v1.3 (Baselga & Orme, 2012) to determine whether the ecological
214 differences between sampling units resulted from species turnover (β_{Sim}) or nestedness (β_{Sne}).
215 Turnover measures the replacement of species between sites caused by environmental
216 differences, disturbance, or competition. Nestedness is a loss of species between sites, usually
217 due to differences in local conditions or ecological niches, where the species-poorer site contains
218 a subset of the species present in the species-richer site (Legendre, 2014).
219   Null models were used to determine whether beta diversity patterns resulted from either
220 random changes in alpha and gamma diversity, or from underlying deterministic mechanisms in
221 communities or the landscape (Chase et al., 2011). We constructed null models for the beta

222   Raup-Crick index (β_{R-C}) using the algorithm developed by Chase et al. (2011) with 9999
223   randomizations. β_{R-C} compares the observed versus expected beta diversity under the null model,
224   scaling the results to a range between -1 and 1. This value indicates whether the beta diversity
225   observed between windows, or vegetation classes, is more similar (values close to -1), equal
226   (values close to 0), or less similar (values close to 1) than the one expected by chance (β_{R-C} null
227   model). We built a dendrogram and a nonmetric multidimensional scaling (NMDS) plot based on
228   β_{R-C} values for windows and vegetation classes, respectively (Chase et al., 2011). The
229   dendrogram was constructed using the complete linkage method, as it produces clusters with
230   ecological discontinuities (Legendre & Legendre, 2003). We compared the dendrogram and
231   NMDS plot based on β_{R-C} with homologous plots based on *Sørensen* dissimilarity to examine
232   whether deterministic mechanisms are underlying the observed beta diversity across the
233   landscape (Chase et al., 2011). All statistical analyses and models were carried out using R
234   v.3.3.1 (R Development Core Team, 2015).
235
236   **Results**
237
238   We collected a total of 15,457 specimens belonging to 55 species in the eight windows at
239   REBISO (Table S4a). The most abundant species was *Deltochilum mexicanum* (15% of total
240   abundance), followed by *Onthophagus corrosus* (13%), *Eurysternus maya* (12%), *Canthon*
241   *vazquezae* (11%), and *Onthophagus batesi* (8%). Sampling coverage on each window was 99%
242   (Table S4a). However, the sampling coverage of vegetation classes varied between windows: for
243   forest vegetation it ranged from 91% (W6) to 100% (W8), it was over 98% for second-growth
244   forests, and between 95% (W3) and 99% (W6) for pastures (Table S4a).
245
246   **Diversity, Abundance, and Biomass Patterns in Windows**
247
248   Species richness (^{0}D) in the windows sampled ranged from 22 (W1, intact window) to 37 (W4,
249   variegated window), whereas the exponential Shannon diversity index (^{1}D) ranged from 4.9
250   (W2, intact window) to 17.6 (W5, variegated window) species (Table 2). Species richness in W4
251   and W5 was significantly higher than in the other windows (Fig. 2a).
252   *Deltochilum mexicanum*, *E. maya*, and *C. vazquezae* were the most abundant species in
253   intact windows W1 and W2 (Fig S1a); *C. vazqueze*, *E. maya*, and *Eurysternus angustulus* were
254   the most abundant ones in variegated windows W3, W4, and W5; and *O. batesi*, *O. corrosus*, and
255   *Copris lugubris* were the most abundant species in fragmented windows W6, W7, and W8 (Fig
256   S1a). Biomass patterns in the dung beetle communities differed from those observed in their
257   abundance values. *Deltochilum mexicanum*, *E. maya,* and *Ontherus mexicanus* were the
258   dominant species, in terms of biomass, in intact windows W1 and W2 (Fig S1a); *D. mexicanum*,
259   *E. maya*, and *Dichotomius amplicollis* were the dominant species in W3; *D. mexicanum*, *D.*
260   *amplicollis,* and *Dichotomius annae* in W4; and *Coprophanaeus corythus*, *Deltochilum sublaeve,*
261   and *D. amplicollis* in W5. *Coprophanaeus corythus*, *C. lugubris*, and *D. amplicollis* were the
262   species with the highest biomass in fragmented windows W6, W7, and W8 (Fig S1a).

263   The highest abundance values (44-52 individuals per trap) were recorded in the intact
264   windows W1 and W2 (Table 3), followed by fragmented windows W6, W7, and W8 (30-36
265   individuals per trap), and variegated windows W3, W4, and W5 (15-30 individuals per trap).
266   However, these differences were not statistically significant ($\chi^2 = 8.923$; df = 7; P = 0.26; Table
267   3). By contrast, there were significant differences in mean biomass between windows ($\chi^2 =$
268   45.143; df = 7; P = >0.001; Table 3). Mean biomass per trap was significantly higher in windows
269   W1 and W2 (8.2-9.1 grams per trap, Table 3), but no significant differences were found between
270   fragmented (2.2-3.7 grams per trap, Table 3) and variegated windows (2.4-3.9 grams per trap,
271   Table 3).
272   All the landscape variables had a significant positive effect on the species richness (^0D) in
273   each window. However, the splitting index was the variable that best explained variations in
274   species richness (Table 4). Although the exponential Shannon diversity (^1D) values were
275   positively related to the splitting index and edge density, the splitting index was the best
276   predictor for variations in Shannon diversity between windows. Edge density and forest cover
277   were the best predictor variables for dung beetle abundance and biomass, respectively; edge
278   density was negatively correlated with abundance, and forest cover positively correlated with
279   biomass (Table 4).
280   True beta diversity of orders 0 and 1 indicated two effective communities between
281   windows, $^0\beta$ being slightly smaller than $^1\beta$ (Table 2). The multiple-site Sørensen value calculated
282   for all windows was 0.65 (Fig. 3a "W Total"); 85% of this dissimilarity was due to species
283   turnover (β_{Sim}) and 15% to nestedness-resultant component (β_{Sne}). Sørensen dissimilarity for
284   intact windows W1 and W2 was lower than 0.4, mainly due to nestedness (β_{Sne}) (Fig. 3a).
285   Dissimilarity ranged from 0.3 to 0.45 in variegated windows (W3, W4, W5), and from 0.3 to
286   0.58 in fragmented windows (W6, W7, W8). In most cases (except for W8), the observed
287   Sørensen dissimilarity values were primarily due to species turnover (Fig. 3a).
288   The dendrogram based on the *Sørensen* distance revealed two main groups (Fig. 3b). The
289   first group includes the fragmented windows (W6, W7, W8), while the second group reveals a
290   gradient of increasing similarity ranging from the intact (W1, W2) to the variegated (W3, W4,
291   W5) windows. The null-model analysis showed that the difference between fragmented windows
292   with respect to the variegated and intact windows was higher than expected by chance (β_{RC}
293   Value: 1.0, Fig. 3c). However, the dissimilarity between variegated and intact windows did not
294   exceed the null expectation of beta diversity ($0 < \beta_{RC} < 0.3$, Fig. 3c).
295
296   **Diversity, Abundance, and Biomass in Vegetation Classes**
297
298   The dung beetle species richness ($^0D = 34$ species) in pastures was significantly lower than in the
299   other vegetation classes, but there were no significant differences between second-growth and
300   tropical forests (44 and 45 species, respectively) (Fig. 2b). We recorded the lowest exponential
301   Shannon diversity values (^1D) in the tropical forests (7.75) and the highest in second-growth
302   forests (15.54) (Table 2).

303   *Deltochilum mexicanum*, *C. vazquezae*, and *E. maya* were the most abundant species in
304   tropical forest sites (Fig S1b); *O. corrosus, D. mexicanum,* and *E. maya* in the second-growth
305   forest; and *O. batesi*, *O. corrosus*, and *C. lugubris* in pasture sites (Fig S1b). *Deltochilum*
306   *mexicanum*, *E. maya*, and *O. mexicanus* contributed with the highest biomass in tropical forests;
307   *D. mexicanum*, *C. corythus*, and *E. maya* in the second-growth forests (Fig S1b); and *C.*
308   *corythus*, *C. lugubris*, and *D. amplicollis* in pasture sites (Fig S1b).
309   No significant differences in abundance were observed between vegetation classes (χ^2 =
310   3.701; df = 2; P = 0.16, Table 3). The average number of individuals per trap was 37.8 in second-
311   growth forests, followed by tropical forests (30.2) and pasture sites (17.7) (Table 3). By contrast,
312   there were significant differences in mean biomass between vegetation classes (χ^2 = 10.829; df =
313   2; P= 0.004). Pasture sites had a significantly lower mean biomass per trap (2.09 g) than tropical
314   forest (5.05 g) and second-growth forest (4.53) sites, which showed no significant differences
315   between them (Table. 3).
316   According to the multiplicative partition of diversity, there were 2.9 effective
317   communities for $^0\beta$ and 2.5 communities for $^1\beta$ in the three vegetation classes combined. Two
318   effective communities were estimated for both the tropical forest and second-growth forest
319   classes, with $^1\beta$ higher than $^0\beta$ in both cases. Only one effective community was estimated for the
320   pasture class, with $^0\beta$ higher than $^1\beta$ (Table 2). The Sørensen dissimilarity between vegetation
321   classes was 0.85, with 88% of this value accounted for by species turnover (β_{Sim}) and 12% by
322   nestedness processes (β_{Sne}) (Fig. 4b).
323   Tropical forests and second-growth forests showed higher Sørensen values (0.71 and
324   0.70, respectively) than pastures (0.54) (Fig. 4a). The NMDS plot based on the Sørensen distance
325   formed a compact cluster of pasture sites, whereas most of the tropical forest and second-growth
326   forest sites overlapped between themselves and with the pasture sites. (Fig. 4b). The NMDS plot
327   based on the beta Raup-Crick null model index (β_{R-C}) separated the tropical forest sites from
328   pastures, whereas second-growth forest sites overlapped with tropical forest and pasture classes
329   (Fig. 4c).
330
331   **Discussion**
332
333   Our results identify the REBISO as one of the regions with highest diversity of Scarabaeinae in
334   Mexican tropical forests, with 55 species, along with the Chimalapas, Oaxaca, with 74 species
335   (Peralta Moctezuma, 2019); the Lacandon forest, Chiapas, with 49 species (Navarrete & Halffter,
336   2008); and the Tuxtlas forest, Veracruz, with 44 species (Favila, 2005).
337
338   **Local Patterns of Species Richness and Assemblage Structure**
339
340   Dung beetle communities in variegated windows showed the highest richness values in the
341   REBISO. Rös, Escobar & Halffter (2012) and Costa et al. (2017) also found a higher richness of
342   dung beetle species in variegated landscapes. Landscape variegation can be a significant
343   environmental driver of local diversity as it increases the range of habitats available for species

344   by creating a complex composition and configuration (Tscharntke et al., 2012; Ramírez-Ponce et
345   al., 2019). The high species richness and diversity found in variegated windows in the REBISO
346   can be attributed to the convergence of multiple dung beetle assemblages including forest
347   specialists (e.g., *Eurysternus caribaeus*, *Sulcophanaeus chryseicollis,* and *Uroxys boneti*), forest-
348   pasture edge specialists (*O. landolti, Canthon cyanellus*), open habitat specialists (*D. annae, C.*
349   *lugubris, O. corrosus*), and generalist beetles (*O. batesi*) (Favila, 2005; Navarrete & Halffter,
350   2008).
351   Intact and fragmented windows showed lower diversity values than variegated windows.
352   This diversity pattern is consistent with the intermediate disturbance theory (Grime, 1973). Sites
353   with little or no disturbance favor the predominance of highly competitive forest specialists such
354   as *D. mexicanum, C. vazquezae,* and *E. maya,* which accounted for 85% of the total abundance
355   and 90% of the total biomass in intact windows, thus preventing a higher local diversity. On the
356   other hand, the intense landscape changes caused by livestock production in fragmented
357   windows reduce the local species richness of dung beetles since many native-forest species are
358   unable to adapt to the new open habitat conditions (Halffter, Favila & Halffter, 1992; Silva,
359   Storck-Tonon & Vaz-de-Mello, 2016; Alvarado et al., 2018).
360   The presence of the exotic African species *Digitonthophagus gazella* (Montes de Oca &
361   Halffter, 1998) in the REBISO is worth mentioning. Although *D. gazella* was only recorded in
362   pastures of fragmented windows (W6, W7), and contributed with only a small fraction of the
363   community abundance and biomass (six and four percent, respectively), they may pose
364   competitive pressure on native species inhabiting open areas (Lobo & Montes de Oca, 1994).
365   Further studies are needed to assess how this invasive beetle might affect native species in the
366   REBISO.
367   Dung beetles are involved, among other ecological processes, in the recycling of organic
368   matter, soil bioturbation, and secondary seed dispersal (Nichols et al., 2008). The amounts of soil
369   removed, dung buried, and seed dispersed are significantly and positively influenced by the
370   species richness and biomass of dung beetle assemblages (Nunes et al., 2018; Alvarado, Dáttilo
371   & Escobar, 2019). The tropical forest sites showed the highest dung beetle species richness and
372   biomass values. Besides, forest coverage was positively related to dung beetle biomass in the
373   REBISO. Both results indicate that the tropical forest sites likely contain the most functionally
374   efficient dung beetle assemblages, thus emphasizing the importance of forest conservation in the
375   REBISO.
376
377   **Effects of Landscape Composition and Configuration on Dung Beetle Assemblages**
378
379   Previous studies conducted in tropical ecosystems have identified landscape composition as the
380   main predictor of the diversity of dung beetle assemblages (Sánchez-de-Jesús et al., 2016;
381   Alvarado et al., 2018). However, in our study, landscape fragmentation was the primary
382   explanatory variable of variations in species richness and diversity. These findings are likely due
383   to the variegated structure of the REBISO landscape and its "biodiversity-friendly" matrix of
384   second-growth forest (see Perfecto & Vandermeer, 2008; Melo et al., 2013). First, second-

385   growth forests in the REBISO are structurally similar to forest habitats (Ramírez-Marcial et al.,
386   2017). Therefore, while many dung beetle species are restricted to forest patches, others may
387   persist and use the second-growth forest matrix to move between forest patches (Díaz, Galante &
388   Favila, 2010). Second, fragmentation in variegated environments creates conditions that allow
389   the coexistence of species from different habitat types (e.g., forest species, pasture species, edge
390   specialist species), thereby increasing the diversity of dung beetles at the landscape scale
391   (Villada-Bedoya et al., 2016; Fahrig, 2017).
392   Not all fragmentation effects are beneficial since a higher edge density can have adverse
393   effects on the abundance, biomass, and even the physiological condition of tropical dung beetles
394   (Portela Salomão et al., 2018). We found the lowest abundance of dung beetles in variegated
395   windows, where the highest edge density occurs. A higher edge density is coupled with less
396   habitat area, limiting the capacity of the landscape to support medium- and large-sized mammal
397   species. Pozo-Montuy et al. (2019) observed that medium- and large-sized mammals are
398   significantly less abundant and diverse in the REBISO buffer zone (i.e., where the variegated
399   windows are located). Such reduction in mammal density can cause a marked decrease in dung
400   quantity and availability, thus limiting the growth of dung beetle populations (Nichols et al.,
401   2009). Also, microclimatic conditions such as temperature and relative humidity are more
402   variable in forest edges, which might negatively affect the reproduction and survival of dung
403   beetles (Klein, 1989; Feer, 2013). Our findings suggest that fragmentation processes in
404   variegated windows foster a high dung beetle diversity, but might also limit their population
405   growth due to insufficient resources, reduced habitat area, or sub-optimal microclimatic
406   conditions. Future studies should assess the strength and extent of this trade-off between dung
407   beetle diversity and abundance, and its functional consequences across the REBISO.
408
409   **Beta Diversity Patterns and Mechanisms of Diversity Maintenance**
410
411   Species turnover is the primary driver of the high diversity and complementarity of the dung
412   beetle communities found in the REBISO. There were between 3 and 27 species not shared
413   between windows, and from 4 to 35 species not shared between vegetation classes. Each window
414   and vegetation class contributed two or three unique species to the overall diversity. The largest
415   turnover values were found between the fragmented windows (W6, W7, and W8) vs. the
416   variegated and intact windows (W1 to W5), and between the forested vegetation classes (tropical
417   forest, second-growth forest) vs. the pasture sites. The anthropic disturbances and the
418   heterogeneous landscape of REBISO favor this high beta diversity since dung beetles are
419   especially susceptible to environmental variability (Arellano, Leon-Cortes & Halffter, 2008;
420   Costa et al., 2017).
421   The differences observed in the species assemblages of fragmented windows (W6, W7,
422   and W8) and those in the other windows (W1 to W5) are not random. Likewise, the differences
423   between tropical forest and pasture assemblages are not random. Significant deviations from
424   random expectations of beta diversity indicate niche-structured assemblages in which
425   environmental filters determine species membership in a community (Chase et al., 2011; Püttker

426 et al., 2015). Intensive anthropic disturbances such as deforestation can act as an environmental
427 filter in fragmented windows and pastures, selecting stress-tolerant dung beetle species able to
428 survive in open habitats (Halffter, Favila & Halffter, 1992; Spector & Ayzama, 2003; Gardner et
429 al., 2008). *Deltochilum mexicanum*, *C. vazquezae*, *S. chryseicollis*, *Canthon femoralis*, and *E.*
430 *maya* probably are the species most sensitive to the environmental filters caused by anthropic
431 disturbance. Although these forest species are widely distributed in the biosphere reserve
432 (Sánchez-Hernández et al., 2018), their abundance was drastically reduced in fragmented
433 windows.
434   We found signs of biotic homogenization in the pasture sites. For instance, the lowest alfa
435 and beta diversity values were recorded in pastures, and their species assemblages were more
436 similar to each other than expected by chance, regardless of the windows where they were
437 located, indicating shared environmental filtering processes (Chase, 2010). Anthropogenic
438 environmental filters are one of the main drivers of biotic homogenization, eroding alfa and beta
439 diversity and diminishing ecosystem resilience and viability (Gámez-Virués et al., 2015). Hence,
440 the advance of the agricultural frontier in the REBISO landscape should be monitored closely to
441 prevent further biotic homogenization processes among the dung beetle species assemblages.
442   In our study, $^1\beta$ between the intact and variegated windows (W1 to W5), as well as
443 between tropical forests and second-growth forests, was higher than $^0\beta$. Thus, the true beta
444 diversity is mainly due to differences in the abundance of shared species rather than to
445 differences in richness (Jost, 2007). Besides, the overall beta diversity between these windows
446 and vegetation classes was not different from that expected by chance. Most species in neutral
447 communities are considered ecologically equivalent since, in the absence of any factor limiting
448 their dispersal, they can appear at random in any of the null assemblages (Püttker et al., 2015;
449 Ortega-Martínez et al., 2020). Both results suggest that the REBISO still holds sufficient
450 vegetation cover to maintain a continuous flow of dung beetles between forested landscape
451 sections (W1 to W5).
452   Given the significant stochasticity of beta diversity between intact and variegated
453 windows, and between tropical forests and second-growth forests, we can conclude that the
454 landscape variegation in the REBISO does not affect dung beetle diversity negatively. However,
455 it is essential to conserve the forested patches to maintain a high dispersal between sites, thereby
456 increasing the resilience of dung beetle populations to habitat loss and isolation (de Castro Solar
457 et al., 2015; Socolar et al., 2016). Landscape variegation can be an effective strategy to buffer the
458 impact of intense anthropic disturbances (Rös, Escobar & Halffter, 2012; Costa et al., 2017).
459 Variegation can be achieved by maintaining the forest cover and incorporating more
460 biodiversity-friendly production systems, such as agroforestry practices, in the landscape matrix
461 (Perfecto & Vandermeer, 2008).
462
463 **Conclusions**
464

465 This research contributes to better understand how diversity is distributed in variegated
466 landscapes, and the role of heterogeneous landscapes in the conservation and management of
467 tropical biodiversity. Tropical forests and second-growth forests contributed significantly to
468 maintaining the diversity and biomass of dung beetle assemblages. The variegated structure of
469 the landscape fosters a high dung beetle diversity. The heterogeneity of the REBISO landscape
470 favors the formation of complementary dung beetle communities. Both deterministic and
471 stochastic processes drive the beta diversity patterns in the landscape. Intense anthropic
472 disturbances in fragmented windows and pastures act as non-stochastic filters upon dung beetle
473 species, eroding the alpha and beta diversity of these sites. By contrast, random processes govern
474 the less disturbed sites of the REBISO: fragmented tropical forests and second-growth forests.
475 Increasing habitat variegation in highly disturbed sites can be an effective strategy to buffer and
476 prevent further biotic homogenization processes.
477
478

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480

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Figure 1

Study area showing the location of the sampling windows at the Biosphere Reserve Selva El Ocote, Chiapas.

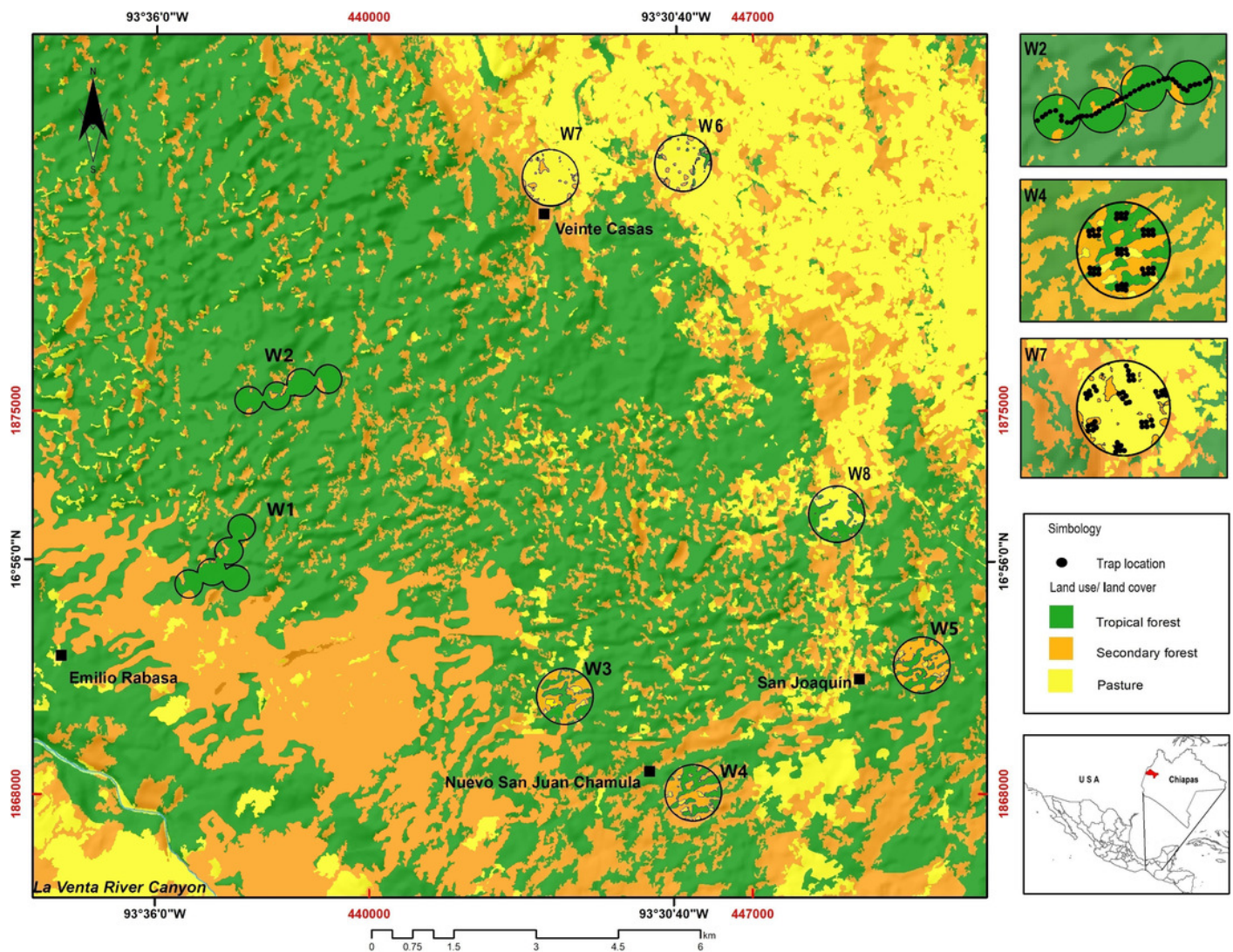



Figure 2

(A) Observed species richness of dung beetles per window (W); (B) Interpolation-extrapolation species accumulation curve per vegetation class.

95% bootstrap confidence intervals are shown for observed richness per window and the species accumulation curves per vegetation class; **(A)** Intact Landscapes: W1, W2; Variegated Landscapes: W3, W4, W5; Fragmented Landscapes: W6, W7, W8; **(B)** Circle: Forest; Triangle: Second-growth forest, Square: Pasture. The red vertical line at the end of the species extrapolation curve of the second-growth forest represents the base sample size for comparison of species richness between vegetation classes.

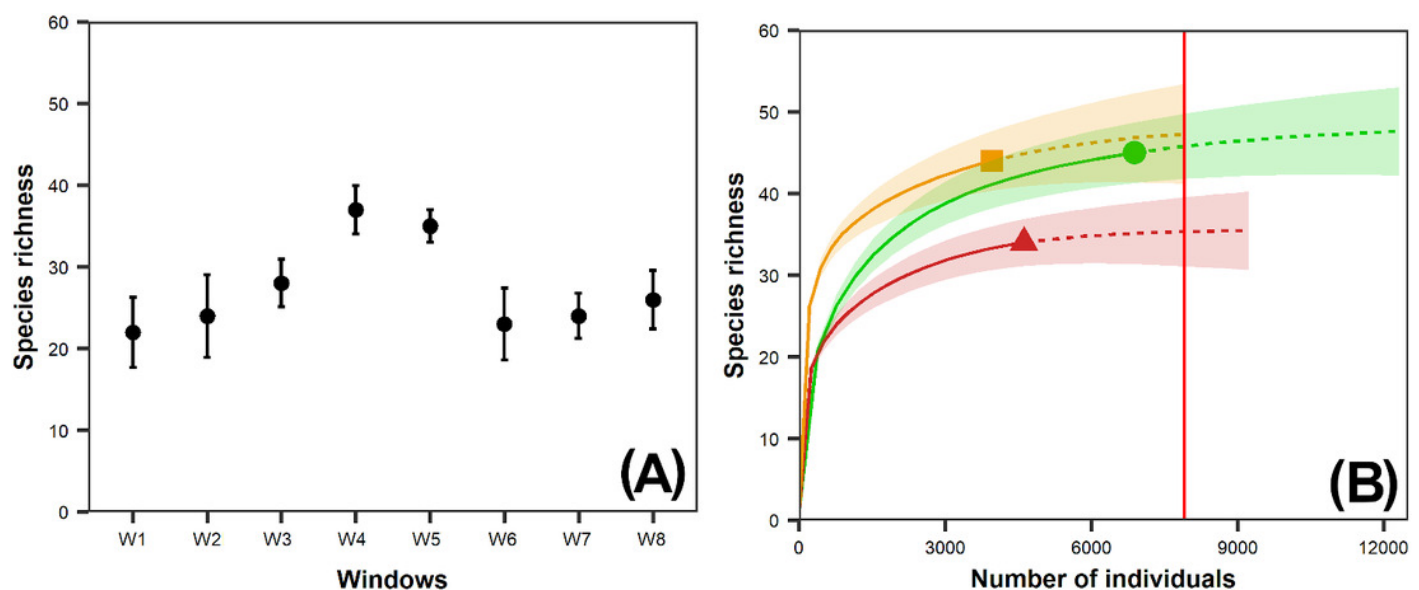



Figure 3

(A) Beta diversity within windows; Dendrogram based on (B) Sørensen dissimilarity between windows & (C) βR-C dissimilarity between windows .

(A) Black dots: Sørensen beta diversity (βSor) between windows. White bars: Percentage contribution of species turnover (βSim) to beta diversity (βSim/βSor); Black bars: Percentage contribution of species-nestedness (βSne) to beta diversity (βSne/βSor).

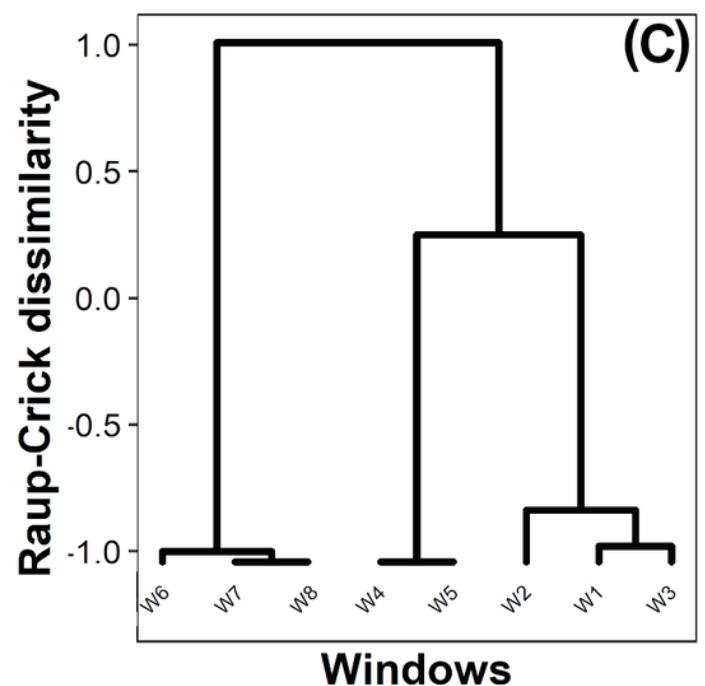
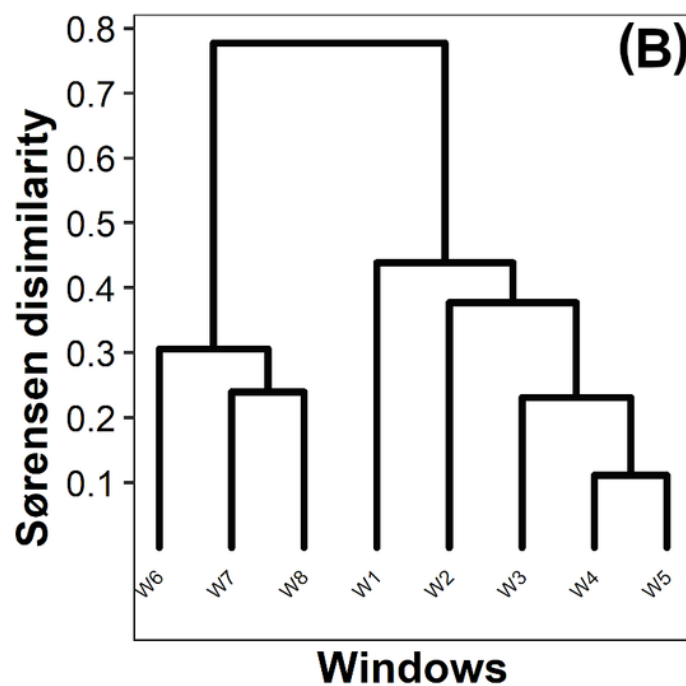
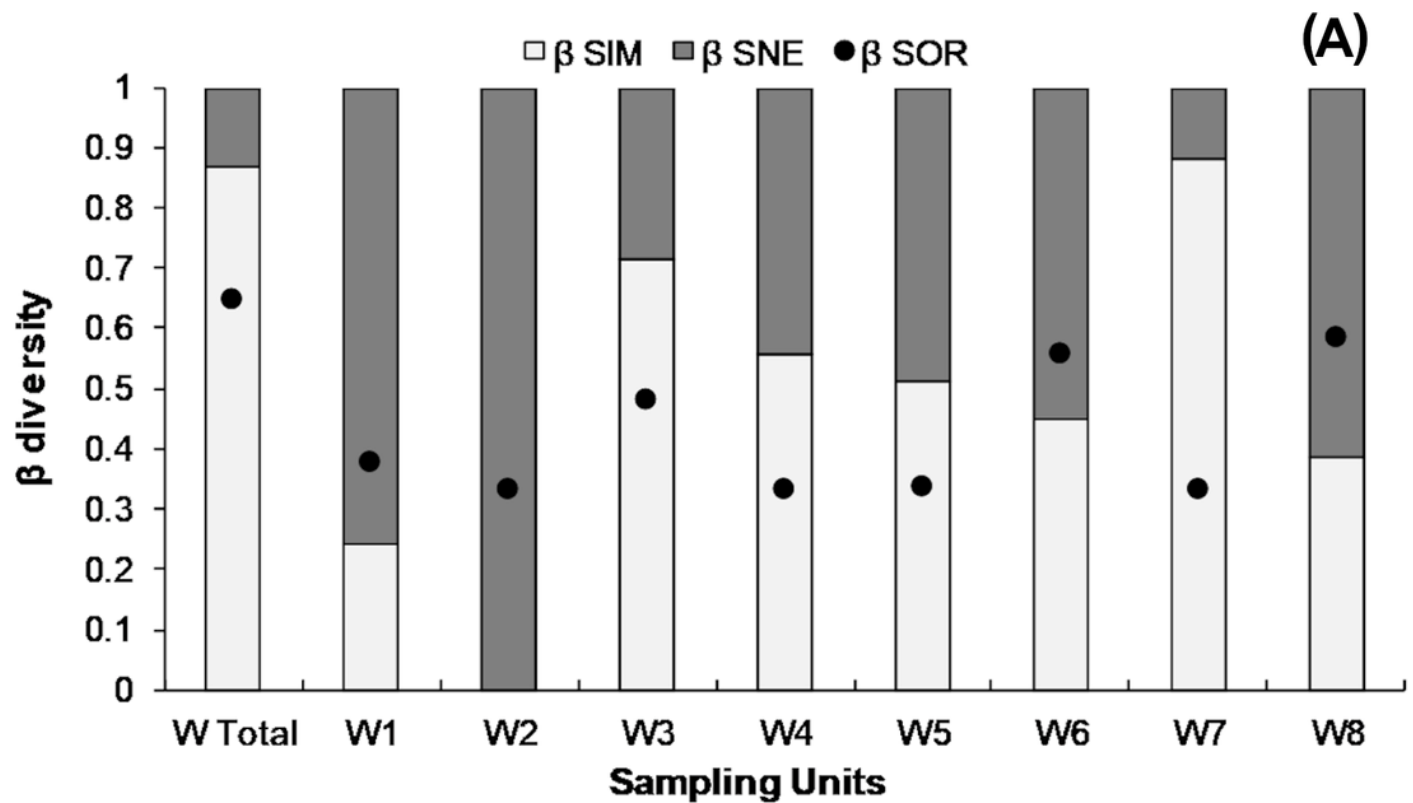



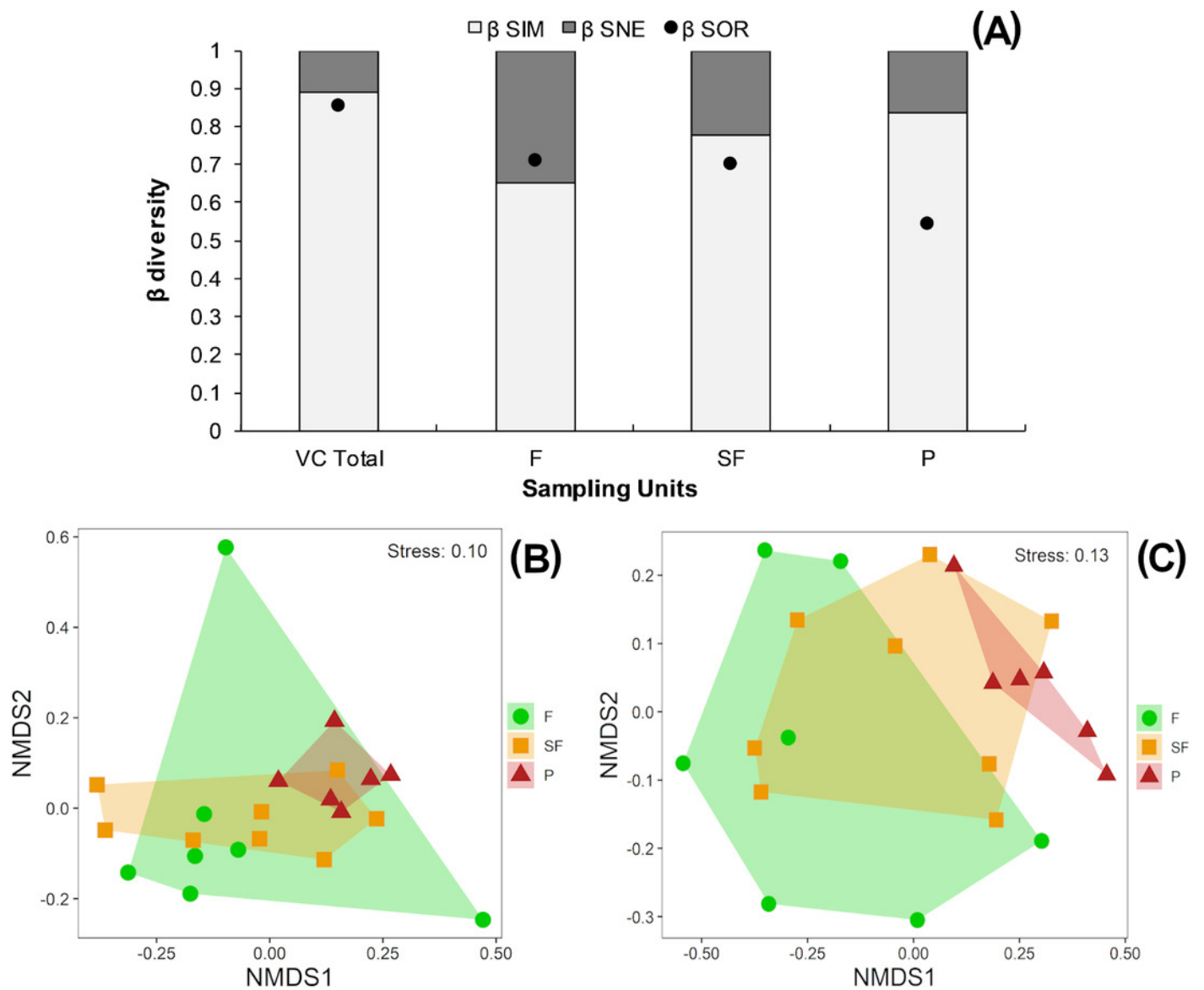
Figure 4

(A) Beta diversity within vegetation classes; Non-metric Multidimensional scaling ordination for vegetation classes based on (B) Sørensen dissimilarity & (C) βR-C dissimilarity.

(A) Black dots: Sørensen beta diversity (βSor) between vegetation classes. White bars:

Percentage contribution of species turnover (βSim) to beta diversity (βSim/βSor), black bars:

Percentage contribution of species-nestedness (βSne) to beta diversity (βSne/βSor); **(B & C)**

F: Forest, SF: Second-growth forest, P: Pasture.

Vegetation classes found at Reserva de la Biosfera Selva El Ocote, Mexico.

Vegetation class	Description
Tropical forest (n=7): [a]38% **W1, W2, W3, W4, W5, W6, W8.**	Forest in a mature successional stage with a dense canopy cover. The most common tree species are *Pseudolmedia spuria*, *Louteridium donnell-smithii*, *Manilkara sapota*, *Swietenia macrophylla* and *Quararibea funebris* (SEMARNAT/CONANP 2001; Ramírez-Marcial et al. 2017). Mean canopy cover, 82.32% (±1.35 s.e.); mean basal area, 912.24 cm^2 (±163.88 s.e.).
Second-growth forest (n=8): [a]30% **W1, W2, W3, W4, W5, W6, W7, W8**	Forest in intermediate successional stage, recovering after 1998 fire; the canopy is less dense than in the tropical forest. Dominated by *Heliocarpus appendiculatus* and *Eugenia acapulcensis* (SEMARNAT/CONANP, 2001; Ramírez-Marcial et al. 2017). Mean canopy cover, 56.76% (± 3.22 s.e.); mean basal area, 577.65 cm^2 (± 105.14 s.e.).
Pasture (n=5): [a]32% **W3, W4, W5, W6, W7, W8**	Pastures are at least ten years old (SEMARNAT/CONANP, 2001). The few trees present are used mainly as shade for cattle. Mean basal area, 874.29 cm^2 (± s.e. 94.60); canopy cover ranges from 2% to 53% ($\bar{x}$ 22.11%, ± s.e 3.03).

1 [a] Mean coverage over the eight windows.

^{0}D and ^{1}D values in each window and vegetation class at Reserva de la Biosfera Selva El Ocote, Mexico.

F: Forest; SF: Second-growth forest; P: Pasture

	^0D				^1D			
	F	SF	P	Species richness	F	SF	P	Exp (Shannon diversity)
W1	22	11	-	22	5.23	4.8	-	5.36
W2	24	12	-	24	5.05	4.27	-	4.97
W3	21	21	11	28	7.71	7.22	5.38	8.69
W4	31	29	20	37	12.39	13.51	13.91	16.49
W5	27	32	19	35	9.88	16.37	9.55	17.59
W6	5	14	19	23	3.50	5.51	6.40	6.57
W7	-	17	19	24	-	8.08	7.38	7.61
W8	2	20	21	26	1.50	3.46	9.51	5.49
γ	45	44	34	55[a]/55[b]	7.75	15.54	8.93	15.84[a]/15.84[b]
α	18.85	19.5	18.66	27.37[a]/18.9[b]	2.93	6.57	7.34	7.09[a]/6.15[b]
β	2.38	2.25	1.87	2.01[a]/2.9[b]	2.64	2.36	1.21	2.23[a]/2.57[b]

1   [a] Overall window diversity, [b] Overall vegetation class diversity.

Mean abundance and biomass (g) per trap (± sd) in each window and vegetation class.

F: Forest; SF: Second-growth forest; P: Pasture. Pairwise comparison results are shown in Table S5. Different letters indicate statistically significant differences between windows and between vegetation classes (P<0.05).

	Mean abundance/trap (±sd)	P < 0.05	Mean biomass/trap (±sd)	P < 0.05
W1	52.94 (11.13)	a	9.07 (1.01)	a
W2	44.95 (0.11)	a	8.20 (0.93)	a, b
W3	20.83 (13.94)	a	2.37 (0.97)	c
W4	15.72 (7.88)	a	2.53 (0.72)	c
W5	29.55 (10.88)	a	3.89 (1.70)	b, c
W6	15.82 (5.12)	a	2.20 (0.49)	c
W7	35.26 (18.29)	a	2.75 (0.05)	c
W8	36.51 (46.98)	a	3.71 (1.22)	b, c
F	30.28 (13.91)	a	5.05 (2.21)	a
SF	37.89 (26.86)	a	4.53 (3.04)	a
P	17.74 (15.56)	a	2.09 (0.62)	b

Estimated parameters of the best-fit General Linear Models (GLMs) for the effect of landscape composition and configuration on species richness, diversity, abundance, and biomass of dung beetles.

The best-fit GLMs for each response variable are shown, ordered from the best to the worst.

Species richness (^0D), exponential Shannon Diversity (^1D), abundance (Ab), biomass (Bm).

FC: % forest cover; SHDI: landscape diversity; PLAND: percentage of each vegetation class in

a window; SPLIT: splitting index; ED: edge density; D^2: explained deviance.

GLMs	Parameters	Estimate	S.E.	t value	P -value	AICc	D²
$^0D \sim$ SPLIT	Intercept	18.991	0.787	24.110	**< 0.001**	34.955	0.95
	SPLIT	2.696	0.215	12.520	**< 0.001**		
$^0D \sim$ SHDI	Intercept	10.693	5.44	1.965	0.097	53.513	0.47
	SHDI	8.640	2.73	3.161	**0.019**		
$^0D \sim$ ED	Intercept	18.415	3.292	5.593	**0.001**	54.052	0.43
	ED	0.0761	0.025	2.99	**0.024**		
$^0D \sim$ FC	Intercept	27.842	3.221	8.643	**< 0.001**	61.306	0.00
	FC	-0.012	0.063	-0.195	0.851		
$^1D \sim$ SPLIT	Intercept	2.026	1.405	1.443	0.199	44.206	0.79
	SPLIT	2.273	0.384	5.921	**0.001**		
$^1D \sim$ ED	Intercept	1.570	3.202	0.490	0.641	53.606	0.34
	ED	0.064	0.025	2.584	**0.041**		
$^1D \sim$ SHDI	Intercept	-3.447	5.951	-0.579	0.583	54.947	0.22
	SHDI	6.496	2.989	2.173	0.073		
$^1D \sim$ FC	Intercept	9.628	2.879	3.344	**0.015**	59.510	0.00
	FC	-0.014	0.056	-0.248	0.812		
Ab $\sim$ ED	Intercept	4.047	0.308	13.146	**< 0.001**	16.136	0.28
	ED	-0.006	0.002	-2.387	0.05		
Ab $\sim$ SHDI	Intercept	4.524	0.554	8.164	**< 0.001**	16.968	0.20
	SHDI	-0.593	0.278	-2.131	0.072		
Ab$\sim$ FC	Intercept	3.176	0.243	13.070	**< 0.001**	19.952	0.00
	FC	0.005	0.005	1.123	0.305		
Ab$\sim$ SPLIT	Intercept	3.648	0.314	11.629	**< 0.001**	20.222	0.00
	SPLIT	-0.086	0.086	-1.009	0.32		
Bm $\sim$ FC	Intercept	1.752	0.696	2.517	**0.045**	36.795	0.70
	FC	0.064	0.014	4.678	**0.003**		
Bm $\sim$ ED	Intercept	8.037	1.6780	4.785	**0.003**	43.284	0.32
	ED	-0.032	0.013	-2.528	**0.044**		
Bm$\sim$ SHDI	Intercept	9.910	3.346	2.962	**0.025**	45.773	0.08
	SHDI	-2.970	1.681	-1.767	0.127		
Bm$\sim$ SPLIT	Intercept	5.114	1.851	2.763	**0.032**	48.624	0.00
	SPLIT	-0.302	0.506	-0.597	0.572		