

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

Jose D. Rivera ^{Corresp., 1, 2}, **Benigo Gómez** ¹, **Darío A. Navarrete-Gutiérrez** ³, **Lorena Ruíz-Montoya** ¹, **Leonardo Delgado Castillo** ⁴, **Mario E. Favila** ²

¹ Conservación de la Biodiversidad, El Colegio de la Frontera Sur, San Cristóbal de las Casas, Chiapas, México

² Red de Ecoetología, Instituto de Ecología, A.C., Xalapa-Enriquez, Veracruz, México

³ Laboratorio de Análisis de Información Geográfica y Estadística, El Colegio de la Frontera Sur, San Cristóbal de las Casas, Chiapas, México

⁴ Red de Biodiversidad y Sistemática, Instituto de Ecología, A.C., Xalapa-Enriquez, Veracruz, México

Corresponding Author: Jose D. Rivera

Email address: jdr495@hotmail.com

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

Jose D. Rivera^{1, 2}, Benigno Gomez¹, Dario A. Navarrete-Gutiérrez³, Lorena Ruiz-Montoya¹, Leonardo Delgado⁴, Mario E. Favila²

¹ Departamento Conservación de la Biodiversidad, El Colegio de la Frontera Sur, San Cristóbal de las Casas, Chiapas, México

² Red de Ecoetología, Instituto de Ecología A.C., Xalapa-Enríquez, Veracruz, México

³ Laboratorio de Análisis de Información Geográfica y Estadística, El Colegio de la Frontera Sur, San Cristóbal de las Casas, Chiapas, México

⁴ Red de Biodiversidad y Sistemática, Instituto de Ecología A. C., Xalapa-Enríquez, Veracruz, México

Corresponding Author:

Jose D. Rivera¹

Carretera antigua a Coatepec No. 351, El Haya, Xalapa-Enríquez, Veracruz, 91073, México

Email address: jdr495@hotmail.com

Abstract

We studied alpha and beta diversity patterns and their maintenance mechanisms in dung beetle assemblages at Selva El Ocote Biosphere Reserve (REBISO) using landscape windows and vegetation classes. Windows were categorized as intact, variegated, or fragmented, based on the percent loss of tropical forest cover in the landscape. Vegetation classes were tropical forest, secondary vegetation, and pasture. The highest species richness was recorded in variegated windows (28-37 species) and tropical forest (45 species), while the lowest values were found in intact windows (22-24 species) and pasture (34 species). Landscape heterogeneity at Selva El Ocote facilitates the formation of complementary dung beetle communities; thus, beta diversity is the main component of overall diversity at Selva El Ocote. Beta diversity is mainly due to the random turnover of species between intact and variegated windows, and between tropical forests and secondary vegetation; this suggests a high level of connectivity in the landscape. However, the intense disturbance in fragmented windows generates non-stochastic filters on the dung beetle communities, eroding alpha and beta diversity. Increasing the habitat variegation of fragmented sites can be an effective strategy to prevent or ameliorate homogenization processes in Selva El Ocote Biosphere Reserve.

Introduction

Anthropized landscapes encompass a complex combination of natural and semi-natural habitats, where some species can thrive while others may go locally extinct (de Castro Solar et al., 2015). Today, almost 90% of remaining tropical forests are located within anthropized landscapes (Chazdon et al., 2009). As a result, these landscapes now play a crucial role in biodiversity conservation agendas (DeClerck et al., 2010). To implement correct management actions, it is imperative to understand how species diversity responds to anthropized landscapes (Gardner et al., 2009; Socolar et al., 2016), especially given the multiple successional pathways and disturbance states that anthropized landscapes can follow (Fischer & Lindenmayer, 2007; Arroyo-Rodríguez et al., 2017). A landscape-level approach in biodiversity studies incorporates the effects of the multiple landscape components on local and regional biodiversity (Lindenmayer, McIntyre & Fischer, 2003; Gardner et al., 2009; Hodder et al., 2014).

Landscape studies provide information useful for effective natural resource management since many anthropogenic drivers of biodiversity loss, e.g., land-use change or habitat destruction, operate at the landscape level (Hodder et al. 2014). McIntyre and Barret (1992) have coined the variegation concept for anthropized landscapes exhibiting disturbance and vegetation cover gradients. McIntyre and Hobbs (1999) then added the fragmentation concept to the variegation model. These authors classified the landscape into four categories based on the percentage of remaining original vegetation (OV) and the intensity of habitat transformation: 1) Intact landscapes (>90% OV), sites with little or no modification; 2) variegated landscapes (60-90% OV) showing either gradual or abrupt limits between their component units; 3) fragmented landscapes (10-60% OV), characterized by a high degree of modification; and 4) relict landscapes (<10% OV), showing severe modification and almost no forest cover remnants.

The Selva El Ocote Biosphere Reserve (REBISO, hereafter) harbors some of the most heterogeneous, although highly disturbed, remnants of tropical forest in Mexico (Flamenco-Sandoval, Martínez Ramos & Masera, 2007). Frequent forest fires, in addition to the complex geological nature, climate features, and socio-economic dynamics (livestock and agricultural activities) in REBISO have led to a complex and diffuse landscape comprising a mosaic of tropical forests, secondary vegetation, pastures, and croplands (Ochoa, 1996; SEMARNAT/CONANP, 2001; Flamenco-Sandoval, Martínez Ramos & Masera, 2007; Ramírez-Marcial et al., 2017). Thus, a landscape-level approach seems appropriate for examining how species respond to anthropogenic disturbance in REBISO, given its complex and heterogeneous landscape.

Dung beetles (Scarabaeidae: Scarabaeinae) are ideal bioindicators to assess the effects of changes in landscape on diversity (Favila and Halffter 1997, Nichols et al. 2007). Previous studies have shown how habitat loss leads to abrupt changes in the composition and structure of dung beetle communities (Klein, 1989; Quintero & Roslin, 2005; Nichols et al., 2007; Navarrete & Halffter, 2008; Díaz, Galante & Favila, 2010; Cajaiba et al., 2017). However, few studies have evaluated the response of dung beetle communities to disturbance at the landscape level (e.g., Numa et al. 2009; Rös et al. 2012; Sánchez-de-Jesús et al. 2016; Alvarado et al. 2018), or if the observed diversity patterns are stochastic or determined by environmental filters or competitive exclusion between species (Ortega-Martínez et al., 2020). Assessing dung beetle biodiversity at a landscape level, employing multiple but complementary metrics could provide a more comprehensive view of how management schemes contribute to species conservation and diversity maintenance in anthropized landscapes.

In this study we evaluate how the diversity, abundance, and biomass of dung beetles vary across the heterogeneous tropical landscape of Selva El Ocote Biosphere Reserve. We address the following questions: (1) How do the diversity and structure of dung beetle assemblages vary across the REBISO landscape? (2) Do dung beetle assemblages change with the type and proportion of vegetation classes in the landscape? (3) How does beta diversity change and is maintained across the landscape and between different vegetation classes? The information obtained in this study might be useful for designing conservation strategies in complex tropical landscapes with different heterogeneity levels.

Materials & Methods

Study Area

The study was carried out at REBISO, located in the municipalities of Ocozacoautla de Espinosa and Cintalapa, Chiapas (16°45'42"-17° 09' 00" N and 93° 54' 19"-93° 21' 20" W, Fig. 1). The area is mostly underlain by dolomite rocks and limestone, with a dominance of water-soluble sedimentary rocks (Domenici, 2016). The predominant climate types are warm, humid (climate type Am) and warm, subhumid (climate type Am(f)), with mean annual temperature of 22 °C and heavy rainfall throughout the year (SEMARNAT/CONANP, 2001).

A vegetation map of REBISO was produced from a multispectral SPOT6 image acquired in 2014, using a supervised classification method in QGIS v2.12.3 (QGIS Development Team, 2016). The vegetation classes considered were tropical forest, secondary vegetation, and pasture (Fig. 1, Table 1).

Sampling Design

Eight 1-km² (100 ha) sampling windows were established in order to capture the landscape heterogeneity in REBISO (Sánchez-de-Jesús et al., 2016). Each window was separated from each other by at least 2 km to ensure spatial independence between them (Sánchez-de-Jesús et al., 2016). The landscape composition in each window (Table S1) was evaluated with FRAGSTAT v4.2.1 (McGarigal et al. 2012). Based on the percent cover of tropical forest (F), windows were classified as intact (W1, W2; $F > 90\%$), variegated (W3, W4, and W5; $60\% < F < 90\%$), or fragmented (W6, W7, and W8; $10\% < F < 60\%$).

Dung beetles were sampled during the dry (March to May) and the rainy (July-August) seasons of 2016 using pitfall traps. Each trap consisted of a 1 L cylindrical plastic container with 300 ml of ethylene glycol as preservative, buried at ground level and covered with a plastic lid to protect the bait from rain and sun radiation. Pitfall traps were baited with 70 g of either an 80:20 mixture of pig and human feces (copro-traps) or squid flesh (necro-traps) to collect dung and carrion beetles, respectively. Seven sampling sites were established in each window, separated 250-360 meters from each other, to proportionally sample its vegetation class composition (Table S2). Proportional sampling is a suitable method for detecting changes in beta diversity in heterogeneous landscapes (Schoereder et al., 2004). In each sampling site, three copro-traps and three necro-traps (42 traps/window), were placed in a rectangular area separated 50 m from each other to minimize interference between them (Larsen & Forsyth, 2005). The rectangular layout of some trap sets had to be modified in some cases due to the topographic characteristics of the sites. These pitfall traps were left active for 48 hours; the specimens collected were counted, identified to species, and deposited in the entomological collection of El Colegio de la Frontera Sur, San Cristóbal de Las Casas. Field collections in the REBISO were performed with the permission of the Secretaria de Medio Ambiente y Recursos Naturales, Mexico (SGPA/DGS/14214/15).

Data Analysis

We followed a spatial and structural approach (*sensu* Rös et al. 2012) to analyze the data. Windows were the sampling units for the spatial approach, while vegetation classes within windows were the sampling units for the structural approach (*sensu* Rös et al. 2012). The sampling completeness of each window and vegetation class was determined using the coverage estimator of Chao and Jost (2012), which allows comparing species diversity across multiple sites (Chao & Jost, 2012).

Alpha diversity in each sampling unit (window or vegetation class) was evaluated using the 0D and 1D diversity numbers. 0D is equivalent to species richness and is insensitive to the species abundance (Jost, 2006); 1D is equivalent to the Shannon diversity index and accounts for the most abundant species in a community (Jost, 2006).

Differences in species diversity between windows were examined with a pooled species-accumulation curve using EstimateS v 9.1 (Colwell, 2013). This curve represents the diversity that would be theoretically observed by randomly sampling the landscape up to a given number of individuals (Gotelli & Colwell, 2011); it shows how diversity is distributed in complex landscapes (Rös et al. 2012). Observed diversity values that fall beyond the 95% confidence intervals of the curve are considered to be significantly lower or higher than the expected diversity (Gotelli & Colwell, 2011; Rös, Escobar & Halffter, 2012). Differences in species diversity between vegetation classes were examined using interpolation–extrapolation curves with iNEXT v2.0.11 (Hsieh, Ma & Chao, 2016). Rank-abundance and biomass curves were constructed to compare the proportional contribution of each species in the assemblages present in windows and vegetation classes.

Generalized linear models were used to assess differences in abundance and biomass between windows and vegetation classes. A negative binomial error distribution was selected for abundance data to allow for overdispersion. Log-transformed biomass data were analyzed using a Gaussian error distribution (Crawley, 2013). Pairwise comparisons using Tukey’s test were carried out, with the multcomp package, whenever significant differences were detected (Hothorn et al., 2016).

True beta diversity was estimated by means of the multiplicative partitioning method (Jost, 2007). The *Sørensen* dissimilarity index was partitioned as $\beta_{Sor} = \beta_{Sim} + \beta_{Sne}$ using Betapart v1.3 (Baselga & Orme, 2012) to determine whether the ecological differentiation between sampling units resulted from species turnover (β_{Sim}) or nestedness (β_{Sne}).

Null models were used to determine whether beta diversity patterns resulted from either random changes in alpha and gamma diversity, or underlying deterministic mechanisms in communities or the landscape (Chase et al., 2011). Null models for the beta Raup-Crick index (β_{R-C}) were constructed using the algorithm developed by Chase et al. (2011) with 9999 randomizations. β_{R-C} compares the observed versus expected beta diversity under the null model, scaling the results to a range between -1 and 1. This value indicates whether the diversity between windows, or vegetation classes, is more similar (values close to -1), equally dissimilar (values close to 0), or less similar (values close to 1) than the one expected by chance (β_{R-C} null model). A dendrogram and a nonmetric multidimensional scaling (NMDS) plot based on β_{R-C} values were built for windows and vegetation classes (Chase et al., 2011). The dendrogram was constructed using the complete linkage method, as it produces clusters with ecological discontinuities (Legendre & Legendre, 2003).

No significant spatial structure was detected on the overall data (Table S3) according to Moran I test, implemented with LetsR package (Vilela & Villalobos, 2015). All statistical analysis and models were carried out using R v.3.3.1 (R Development Core Team, 2015).

Results

A total of 15,457 specimens belonging to 55 different species were collected in the eight windows at REBISO (Table S4a). The most abundant species was *Deltochilum mexicanum* (15% of total abundance), followed by *Onthophagus corrosus* (13%), *Eurysternus maya* (12%), *Canthon vazquezae* (11%), and *Onthophagus batesi* (8%). Sampling coverage on each window was 99% (Table S4a). Sampling coverage on the forest vegetation class ranged from 91% (W6) to 100% (W8); it was over 98% on secondary forests, and between 95% (W3) to 99% (W6) on pastures (Table S4a).

Diversity, Abundance and Biomass Patterns in Windows

Species richness (0D) in the windows sampled ranged from 22 (W1, intact window) to 37 (W4, variegated window), whereas the Shannon diversity index (1D) ranged from 4.9 (W2, intact window) to 17.6 (W5, variegated window) species (Table 2). Species richness in most sampling windows was significantly lower than that expected from a random sample of the landscape, except for the variegated windows W4 and W5 (Fig. 2a). *Deltochilum mexicanum*, *E.maya*, and *C. vazquezae* were the most abundant species in intact windows W1 and W2 (Fig 3a); *C. vazqueze*, *E. maya*, and *Eurysternus angustulus* were the most abundant ones in variegated windows W3, W4, and W5; and *O. batesi*, *O. corrosus*, and *Copris lugubris* were the most abundant species in fragmented windows W6, W7, and W8 (Fig. 3a). Biomass patterns in the dung beetle communities differed from the abundance values. *Deltochilum mexicanum*, *E. maya*, and *Ontherus mexicanus* were the dominant species (in terms of biomass) in intact windows (Fig. 3a); *D. mexicanum*, *E. maya*, and *Dichotomius amplicollis* contributed to the largest fraction of the community biomass in W3; *D. mexicanum*, *D. amplicollis* and *Dichotomius annae* in W4; and *Coprophanaeus corythus*, *Deltochilum sublaeve* and *D. amplicollis* in W5. *Coprophanaeus corythus*, *C. lugubris*, and *D. amplicollis* were the species with the highest biomass in fragmented windows (Fig. 3a).

The highest abundance values (44-52 individuals per trap) were recorded in the intact windows W1 and W2 (Table 3), followed by fragmented windows W6, W7, and W8 (30-36 individuals per trap), and variegated windows W3, W4, and W5 (15-30 individuals per trap). However, these differences were not statistically significant ($F = 1.029$; $df = 7$; $P = 0.45$; Table 3). By contrast, there were significant differences in mean biomass between windows ($F = 6.449$; $df = 7$; $P = 0.002$; Table 3). Mean biomass per trap was significantly higher in windows W1 and W2 (8.2-9.1 grams per trap, Table 3), but no significant differences were found between fragmented (2.2-3.7 grams per trap, Table 3) and variegated windows (2.4-3.9 grams per trap, Table 3).

True beta diversity of orders 0 and 1 indicate two effective communities between windows, $^0\beta$ being slightly smaller than $^1\beta$ (Table 2). The Sørensen value calculated for all windows pooled together was 0.65 (Fig. 3b “W Total”); 85% of this dissimilarity was due to

species turnover (β_{Sim}) and 15% to nested processes (β_{Sne}). Sørensen dissimilarity for intact windows W1 and W2 was lower than 0.4, mainly due to nested processes (β_{Sne}) (Fig. 3b). Dissimilarity ranged from 0.3 to 0.45 in variegated windows (W3, W4, W5), and from 0.3 to 0.58 in fragmented windows (W6, W7, W8). In most cases (except for W8), the observed Sørensen dissimilarity values were primarily due to species turnover (Fig. 3b).

The null-model analysis showed that the dissimilarity between fragmented (W6, W7, W8) windows with respect to variegated (W3, W4, W5) and intact windows (W1, W2) was higher than expected by chance (β_{RC} Value: 1.0, Fig. 3c). However, the dissimilarity between variegated and intact windows did not exceed the null expectation of beta diversity ($0 < \beta_{RC} < 0.3$, Fig. 3c).

Diversity, Abundance and Biomass in Vegetation Classes

The dung beetle species richness in pastures was significantly lower vs. the other vegetation classes, but there were no significant differences between secondary vegetation and tropical forest (Fig. 2b). The lowest Shannon diversity values were recorded in the tropical forest windows, and the highest in pasture windows (Table 2). *Deltochilum mexicanum*, *C.vazquezae*, and *E. maya* were the most abundant species in tropical forest sites (Figure 4a); *O. corrosus*, *D. mexicanum*, and *E. maya* in secondary forest (Fig. 4a); and *Onthophagus batesi*, *O. corrosus*, and *C. lugubris* in pasture sites (Fig. 4a). *Deltochilum mexicanum*, *E. maya*, and *O. mexicanus* contributed with the highest biomass in tropical forest; *D. mexicanum*, *C.corythus*, and *E. maya* in secondary forest (Fig. 4a); and *C. corythus*, *C. lugubris*, and *D. amplicollis* in pasture sites (Fig. 4a).

No significant differences in abundance were observed between vegetation classes ($F = 1.694$; $df = 2$; $P = 0.21$, Table 3). However, the average number of individuals per trap was higher (37.8) in secondary forests, followed by forests (30.2) and pasture sites (17.7) (Table 3). On the other hand, there were significant differences in mean biomass between vegetation classes ($F = 5.415$; $df = 2$; $P = 0.01$). Pasture sites had a significantly lower mean biomass vs. both tropical forest and secondary vegetation sites, which showed no significant differences between them (Table. 3).

There were 2.9 effective communities for ${}^0\beta$ and 2.5 communities for ${}^1\beta$ in the three vegetation classes combined. Two effective communities were estimated for both the tropical forest and secondary vegetation classes, with ${}^1\beta$ higher than ${}^0\beta$ in both cases. On the other hand, only one effective community was estimated for the pasture class, with ${}^0\beta$ higher than ${}^1\beta$ (Table 2). Sørensen dissimilarity between vegetation classes was 0.85, with 88% of this value accounted for by species turnover (β_{Sim}) and 12% by nested processes (β_{Sne}) (Fig. 4b). Tropical forests and secondary vegetation showed higher Sørensen values vs. pastures (Fig. 4b). The NMDS plot based on the beta Raup-Crick null model index (β_{R-C}) separated the tropical forest sites from pastures, whereas secondary vegetation sites overlapped with tropical forest and pasture classes (Fig. 4c).

Discussion

Our results identify the REBISO as one of the regions with highest diversity of Scarabaeinae in Mexican tropical forests, with 55 species, along with the Chimalapas, Oaxaca, with 74 species (Peralta Moctezuma, 2019); the Lacandon forest, Chiapas, with 49 species (Navarrete & Halffter, 2008); and the Tuxtla forest, Veracruz, with 44 species (Favila, 2005). The variegated composition of the landscape maintains the regional diversity of dung beetles mainly through the heterogeneous and stochastic distribution of the species.

Local Patterns of Species Richness and Community Structure

Dung beetle communities in variegated windows showed the highest richness values in REBISO. Rös et al. (2012) and Costa et al. (2017) also found a higher richness of dung beetle species in variegated landscapes. Variegated windows can be an important environmental driver of local diversity as they increase the range of habitats available for species (Ritchie & Olff, 1999; Tscharntke et al., 2012; Ramírez-Ponce et al., 2019).

Fragmented and intact windows showed lower diversity values than variegated windows. These diversity patterns are consistent with Connell's intermediate disturbance theory (Connell, 1978). Sites with little or no disturbance favor the predominance of highly competitive specialists such as *Deltotilum mexicanum*, *Canthon vazquezae*, and *Eurysternus maya*, which accounted for 85% of the total abundance and 90% of the total biomass in intact windows, thus preventing a higher local diversity. On the other hand, the intense landscape changes caused by livestock production in fragmented windows reduce the local species richness of dung beetles since many native-forest species are unable to adapt to the new habitat conditions (Fahrig et al., 2011; Alvarado et al., 2018).

Although we found no significant differences in species diversity between intact and fragmented windows, the species composition of these communities was different. Intact windows are located in the core area of REBISO, where forest cover is best preserved and the beetle community is mainly composed of species typically found in tropical forests, such as *D. mexicanum*, *E.maya*, *Eurysternus caribaeus*, *Sulcophanaeus chryseicollis*, and *Uroxys boneti* (Favila and Halffter 1997, Favila 2005; Ros et al. 2012). By contrast, fragmented windows mostly comprise pastures, which harbor an assemblage of beetle species adapted to such simplified environments, such as *Dichotomius annae*, *Copris lugibris*, *Onthophagus corrosus*, *Onthophagus batesi*, *Onthophagus landolti*, and the exotic African species *Digitonthotophagus gazella* (Montes de Oca & Halffter, 1998; Favila, 2005; Horgan, 2007; Navarrete & Halffter, 2008).

Of the vegetation classes examined, tropical forests showed the highest diversity and biomass values. Both attributes are positively related to the amount of soil removed, dung buried, and seed dispersed by dung beetle communities (Braga et al., 2013; Nervo et al., 2014; Nunes et al., 2018). Hence, tropical forest sites have the highest functional potential in REBISO. Conversely, pastures were characterized by a “hyper-abundance” of small (low biomass) dung beetle species (e.g., *Onthophagus landolti*, *Onthophagus corrosus*, *Onthophagus batesi*).

Although there is some evidence showing that high-density of low-biomass species can compensate for the functional activity of larger dung beetles (Amézquita & Favila, 2010; Alvarado, Dáttilo & Escobar, 2019), more studies are needed to evaluate the extent and context of this functional compensation.

Beta (β) Diversity Profiles and Mechanisms of Maintenance

Species turnover is the main driver of the high diversity and complementarity of the dung beetle communities found in REBISO. There were between 3 and 27 species not shared between windows, and from 4 to 35 species not shared between vegetation classes. In addition, each window and vegetation class contributed two or three unique species to the overall diversity. The heterogeneous anthropic disturbances and the complex landscape of REBISO favor this high beta diversity, since dung beetles are especially susceptible to environmental variability (Navarrete & Halffter, 2008; Filgueiras et al., 2016; Sánchez-de-Jesús et al., 2016; Alvarado et al., 2018).

Our null models provided essential information on how landscape characteristics affect beta diversity profiles. Species turnover between fragmented (W6, W7, and W8) and other windows (W1 to W5) is not a random process; likewise, the differences in diversity between tropical forest and pasture sites are not random. Both results suggest that beta diversity between forested and non-forested sections of the landscape is determined by ecological filters (Püttker et al., 2015). Such filters selectively eliminate dung beetle species with low physiological tolerance to habitat disturbance (such as forest cover loss) from fragmented windows (Spector & Ayzama, 2003; Gardner et al., 2008; Villada-Bedoya et al., 2016).

Deltochilum mexicanum, *C. vazquezae*, *S. chryseicollis*, *Canthon femoralis*, and *E. maya* were likely the species most sensitive to those ecological filters. Although they are broadly distributed in the region (Sánchez-Hernández et al., 2018), their abundance was drastically reduced to one or two individuals in fragmented windows. Ecological filters are one of the main drivers of biotic homogenization, eroding beta diversity and decreasing ecosystem resilience and viability (Gámez-Virués et al., 2015). Furthermore, the advance of the agricultural frontier in REBISO should be monitored closely, as the null models and the low true beta diversity values found in pastures indicate some degree of biotic homogenization in the fragmented sections of the landscape.

In our study, $^1\beta$ between W1 to W5, as well as between tropical forest and secondary vegetation, was higher than $^0\beta$ (i.e., $^1\beta > ^0\beta$). Thus, true beta diversity is mainly due to differences in the abundance of shared species (Jost, 2007; Halffter & Rös, 2013). In addition, species turnover in these sites was random. Both results suggest that REBISO still holds a sufficient vegetation cover to maintain a continuous flow of dung beetles between forested landscape sections (W1 to W5), thereby increasing their population resilience to habitat loss and isolation (de Castro Solar et al., 2015; Socolar et al., 2016).

It is worth noting that species turnover between secondary vegetation and the other vegetation classes was also random. This implies that, in addition to acting as a reservoir for forest beetles, secondary vegetation can also harbor species typical of pasture sites. In this sense,

species typical of open habitats such as *O. corrosus*, *C. lugubris*, *Canthon leechi*, and *O. landolti* were highly abundant in secondary vegetation (see Favila 2005, 2012). However, the importance of these species is still minimal, since together they contribute less than 5% to total biomass in secondary-vegetation communities. Given the significant stochasticity of beta diversity between windows and vegetation classes, it is essential to conserve the forest patches currently existing in the landscape in order to maintain the high biodiversity values observed in this study (Socolar et al., 2016).

Conclusions

The heterogeneity of the landscape in Selva El Ocote Biosphere Reserve favors the formation of complementary dung beetle communities. Tropical forests in the landscape are crucial, since they contribute significantly to the conservation of the diversity and biomass of native dung beetle species. Intense disturbance in fragmented windows produces non-stochastic filters on the dung beetle community, eroding the alpha and beta diversity of these sites. Therefore, increasing the habitat variegation of fragmented sites can be an effective strategy to ameliorate and prevent further biotic homogenization in REBISO. This can be achieved by increasing the vegetation variegation in fragmented landscapes and incorporating more biodiversity-friendly production systems such as agroforestry practices (Gardner et al., 2009; Rös, Escobar & Halffter, 2012; Costa et al., 2017).

Acknowledgements

Special thanks to María Guadalupe Hernández López and Erick Hernández Baltazar for their support during data collection. We thank Paula Enríquez, Alfonso González and Guillermo Ibarra for their valuable comments and suggestions. We thank the communities of Emilio Rabasa, Nuevo San Juan Chamula, San Joaquin and Tierra Nueva for granting access to their land to carry out our fieldwork. We also thank REBISO/CONANP for providing logistic support. José Daniel Rivera's M.Sc. studies at Colegio de la Frontera Sur, San Cristóbal de las Casas, Chiapas, Mexico were kindly supported by scholarships from CONACYT and the Heinrich Böll Stiftung Foundation. María Elena Sánchez-Salazar reviewed the English version of the manuscript.

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Figure 1

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

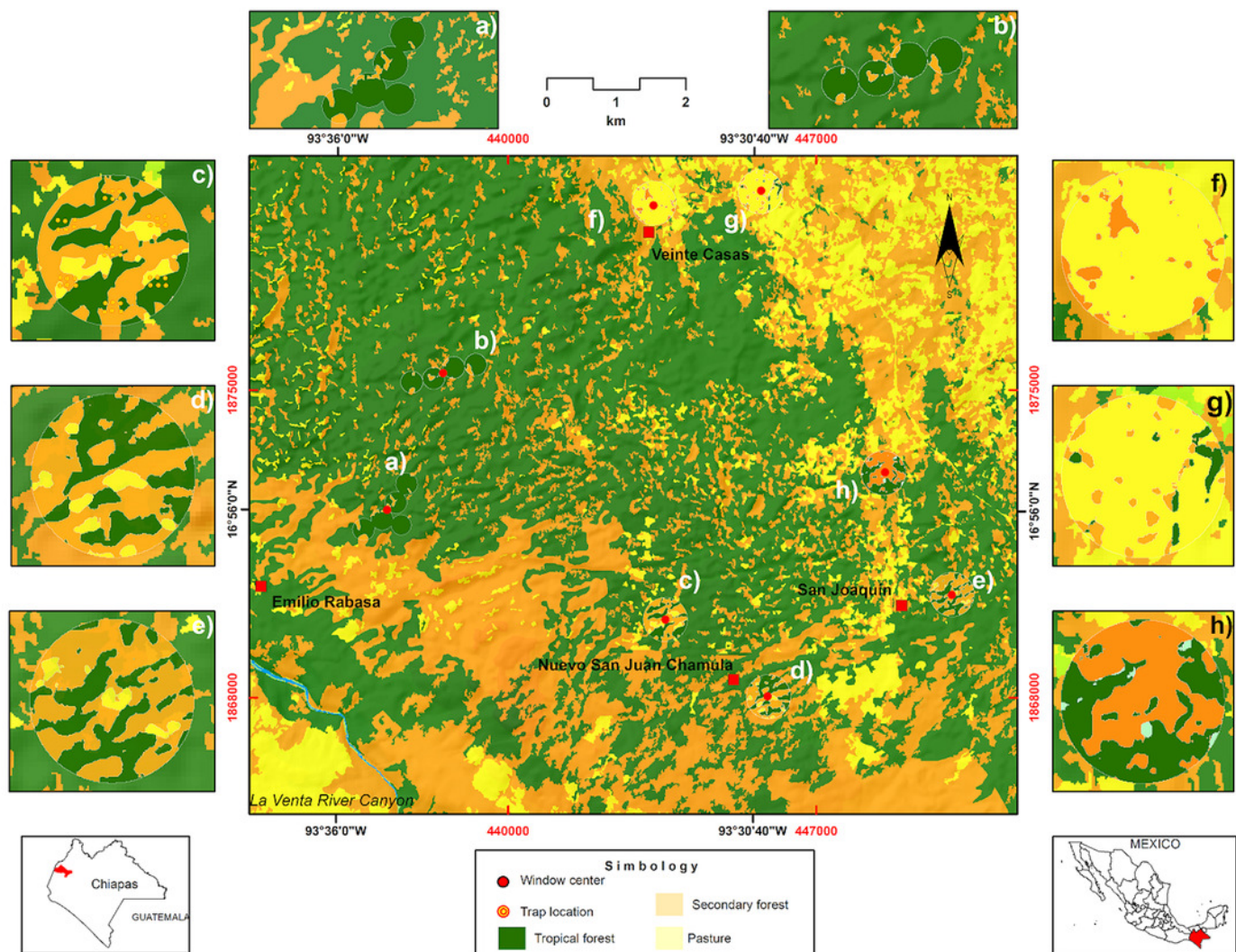


Figure 2

Species accumulation curve between windows and between vegetation classes.

a) Species accumulation curves with 95% confidence intervals, and observed species richness (circle point) of dung beetles per window (W). b) Interpolation-extrapolation species accumulation curve between vegetation classes with 95% confidence intervals; Circle, Forest ; Triangle, Secondary Vegetation; Square, Pasture.

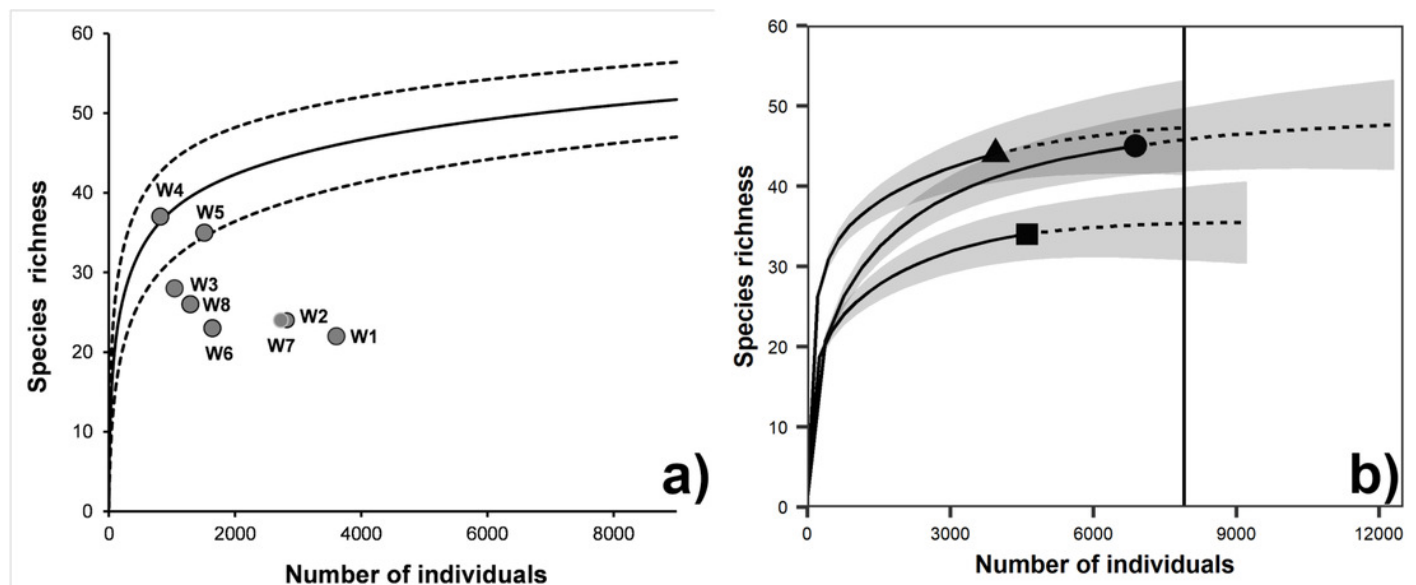


Figure 3

a) Species rank abundance and biomass curves. b) Percentage contribution of species turnover and nestedness to beta diversity between windows. c) β R-C dendrogram between windows.

a) Lines, abundance; dashed lines, biomass; Species identity as in Table S5a. b) Black dots: Sørensen beta diversity (β_{Sor}) between windows, white bars: Percentage contribution of species turnover (β_{Sim}) to beta diversity (β_{Sim}/β_{Sor}), black bars: Percentage contribution of species-nestedness (β_{Sne}) to beta diversity (β_{Sne}/β_{Sor}).

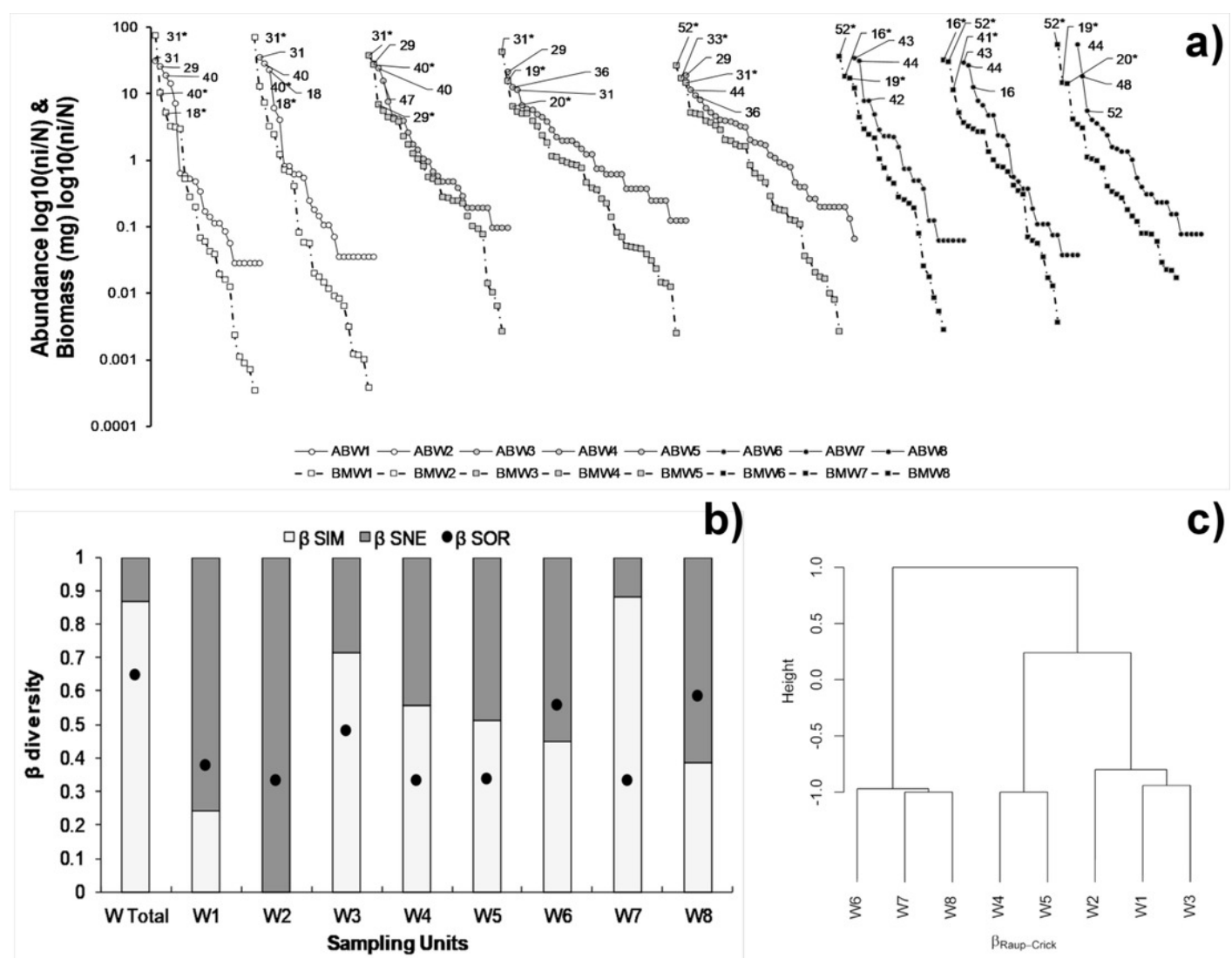


Figure 4

a) Species rank abundance and biomass curves. b) Percentage contribution of species turnover and nestedness to beta diversity between vegetation classes; c) NMDS based on β R-C distance.

a) Lines, abundance; dashed lines, biomass; Species identity as in Table S5a. b) Black dots: Sørensen beta diversity (β Sor) between vegetation classes, white bars: Percentage contribution of species turnover (β Sim/ β Sor), black bars: Percentage contribution of species-nestedness (β Sne/ β Sor). c) Non-metric Multidimensional scaling; Circle, Forest; Triangle, Secondary Vegetation; Square, Pasture.

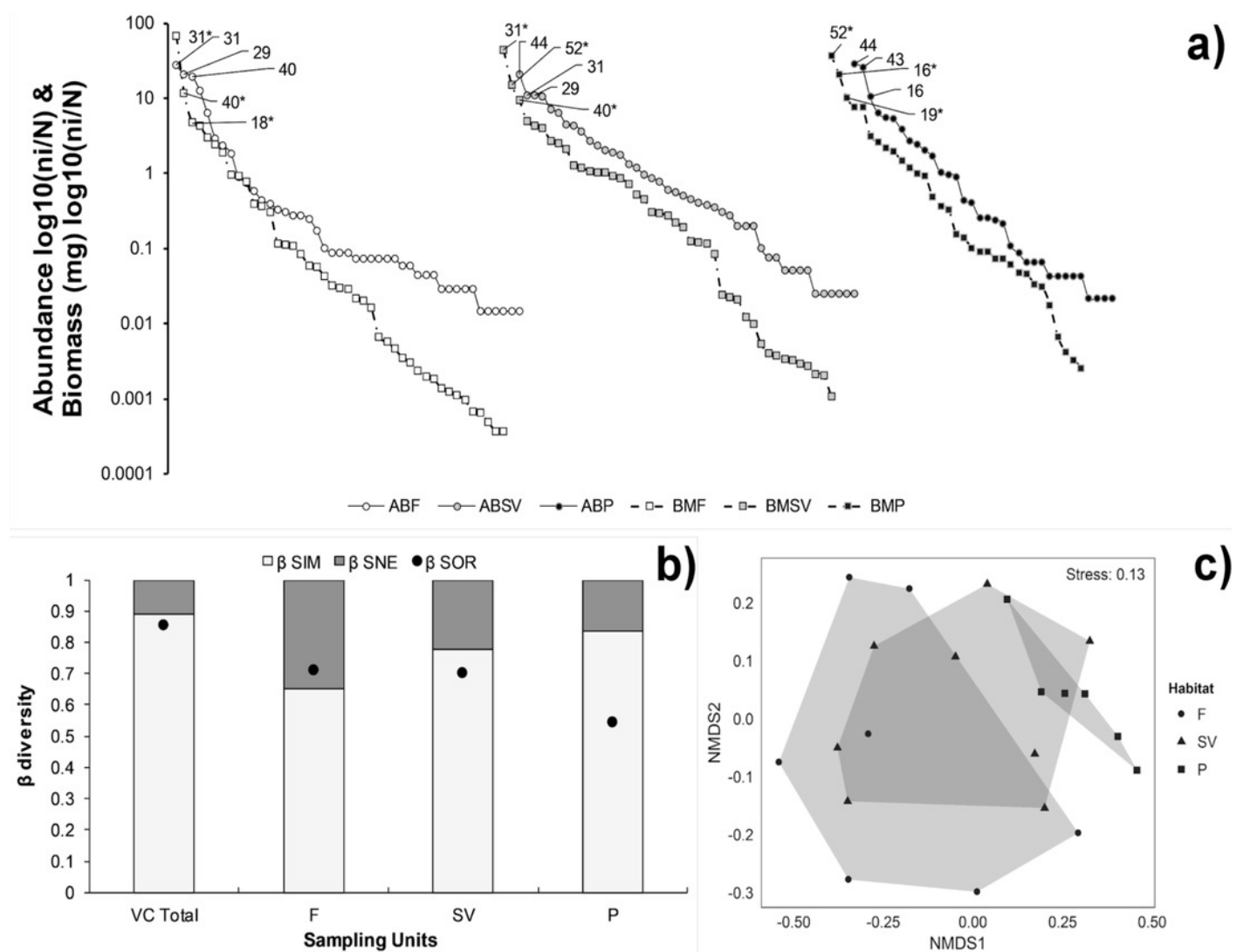


Table 1 (on next page)

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

Vegetation Class	Description
Tropical forest: ^a 38% W1, W2, W3, W4, W5, W6, W8.	Vegetation with dense canopy cover of mature successional stage. The most common tree species are <i>Pseudolmedia spuria</i> , <i>Louteridium donnell-smithii</i> , <i>Manilkara sapota</i> , <i>Swietenia macrophylla</i> and <i>Quararibea funebris</i> (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.).
Secondary Vegetation: ^a 30% W1, W2, W3, W4, W5, W6, W7, W8	Forest in early or intermediate successional stages, recovering after 1998 fire; the canopy is less dense than in tropical forest. Dominated by <i>Heliocarpus appendiculatus</i> and <i>Eugenia acapulcensis</i> (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: ^a 32% W3, W4, W5, W6, W7, W8	Pastures are at least 10 years old (SEMARNAT/CONANP 2001). The few trees present are mainly used as shade for cattle. Mean basal area, 874.29 cm ² (\pm s.e 94.60); canopy cover ranges from 2 % to 53 % (\bar{x} 22.11%, \pm s.e 3.03).

^a Percentage coverage of each vegetation class in the study area.

Table 2(on next page)

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

⁰ D					¹ D			
	F	SV	P	Species richness	F	SV	P	Species richness
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

2 ^a Overall alpha, beta and gamma diversity over all the windows

3 ^b Overall alpha, beta and gamma diversity over all the vegetation classes

4

Table 3(on next page)

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

Significant differences between windows and vegetation classes ($P < 0.05$). GLM results are shown in Table S5.

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

1