



E-ISSN: 2320-7078
P-ISSN: 2349-6800
JEZS 2016; 4(1): 457-463
© 2016 JEZS
Received: 21-11-2015
Accepted: 23-12-2015

Thomas Latha
Dept. of Science, Faculty of
Science and Technology,
University of Belize, University
Drive, Belmopan, Belize, Central
America

Po-Yen Huang
Dept. of Science, Faculty of
Science and Technology,
University of Belize, University
Drive, Belmopan, Belize, Central
America

Grimar Abdiel Perez
Dept. of Science, Faculty of
Science and Technology,
University of Belize, University
Drive, Belmopan, Belize, Central
America

Ishmael Orlando Paquiul
Dept. of Science, Faculty of
Science and Technology,
University of Belize, University
Drive, Belmopan, Belize, Central
America

Correspondence
Thomas Latha
Dept. of Science, Faculty of
Science and Technology,
University of Belize, University
Drive, Belmopan, Belize, Central
America

Dung beetle assemblage in a protected area of Belize: A study on the consequence of forest fragmentation and isolation

Thomas Latha, Po-Yen Huang, Grimar Abdiel Perez, Ishmael Orlando Paquiul

Abstract

Belize is the only Central American country with over 60% forest cover. But recent studies revealed that Belize's forest cover is declining rapidly. Though majority of the forest clearance occurred outside the protected areas, such deforestation activities can cause fragmentation and isolation of forests. Dung beetles are predominantly coprophagous insects that provide important ecological services and are widely used as biological indicators to study the effects of habitat disturbance including fragmentation and isolation. Dung beetle abundance, species richness, beetle size and guild structure was studied in Guanacaste National Park of Belize which is an isolated forest fragment surrounded by anthropogenic habitats. Dung beetles were collected using baited pit fall traps in the months of February, May and August, 2010. A total of 169 beetles belonging to 9 genera and 15 species were collected from the national park. Low abundance, low species richness, dominance of small species and dominance of the generalist species *C. cyanellus cyanellus* indicates that the dung beetle community was adversely affected by fragmentation and isolation.

Keywords: fragmentation, isolation, Guanacaste National Park (GNP), dung beetle, beetle size, functional guild.

1. Introduction

Human led activities such as deforestation, habitat modification and fragmentation are transforming ecosystems around the world. Fragmentation is one of the most commonly occurring environmental transformation in tropical forests [1]. Habitat fragmentation is the process by which large continuous habitat is broken into smaller patches that are isolated from each other by a matrix of habitat types different from the original type [2, 3]. Alteration and fragmentation of forests disrupts ecosystem functioning and is the principal cause of biodiversity losses [4, 5, 6].

Belize is the only Central American country with over 60% forest cover [7]. Studies on Belize's deforestation for the period 1980-2010 estimated Belize's average annual deforestation rate to be under 10,000 ha/year, or 0.6% [8]. But recent satellite imagery study for the period 2010-2012 revealed that Belize's forest cover declined from 62.8% in early 2010 to 61.6% in early 2012 [9]. If the current trend continues within the next 29 years Belize's forest cover would fall to only 50% [9]. This would seriously affect the various ecosystem services they render. Although majority of the deforestation (93.6%) occurred outside the protected areas [9] where land is being converted into agriculture land and plantations [10], such developmental activities can lead to fragmentation and isolation of forest patches which can have serious consequence on the fauna, especially insect communities in these habitats [11, 12].

Dung beetles are widely used as biological indicators to study the effects of habitat disturbance including fragmentation and isolation [1]. Dung beetles are a group of predominantly coprophagous beetles which use dung for feeding and breeding purposes. By burying dung they provide important ecological services such as increase soil fertility [13, 14]; soil permeability and plant growth [13]; seed dispersal [15] and control populations of disease causing parasites [16]. They are important biological indicators and are used to evaluate the effects of habitat disturbance by human activity as they are sensitive to changes in vegetation, microclimate and mammalian fauna of the habitats in which they live [17, 18, 19]. Dung beetles use three broad strategies to feed and breed, each of them serving various ecological functions. Rollers (telecoprids) roll balls of food some distance away from the source and bury them in

vertical tunnels to feed and lay eggs; tunnelers (paracoprids) bury balls of food in vertical tunnels beneath the food source; dwellers (endocoprids) feed and breed within the dung mass [20, 21].

In the present study dung beetle community structure was investigated in an isolated forest fragment of Belize. Present study investigated if fragmentation and isolation affected the species richness (number of species); abundance (number of individuals of all species); beetle size (large vs small beetles) and functional guild composition of dung beetle assemblage in the Guanacaste National Park (GNP) of Belize which is an isolated forest fragment. This research is significant as no study has documented the effects of forest fragmentation on insect communities of Belize. Moreover this study will also provide baseline information on dung beetle community of

Belize as very little studies have been done to document the biodiversity of Belize especially those of insects.

2. Materials and Methods

2.1 Study site

Guanacaste National Park is located 17° 15' 52" N, 88° 47' 10" W at an altitude of 71msl in the Cayo District of Belize (Fig.1). It is the smallest and one of the most accessible national parks in Belize with an area of 58 acre (20.8 ha). The national park is located at the junction of George Price Highway and Hummingbird Highway and 2 miles from the capital City of Belmopan which is situated to the south. It is bordered to the north by the Belize River and to the west by Roaring Creek, a tributary that flows from the Maya Mountains [22].

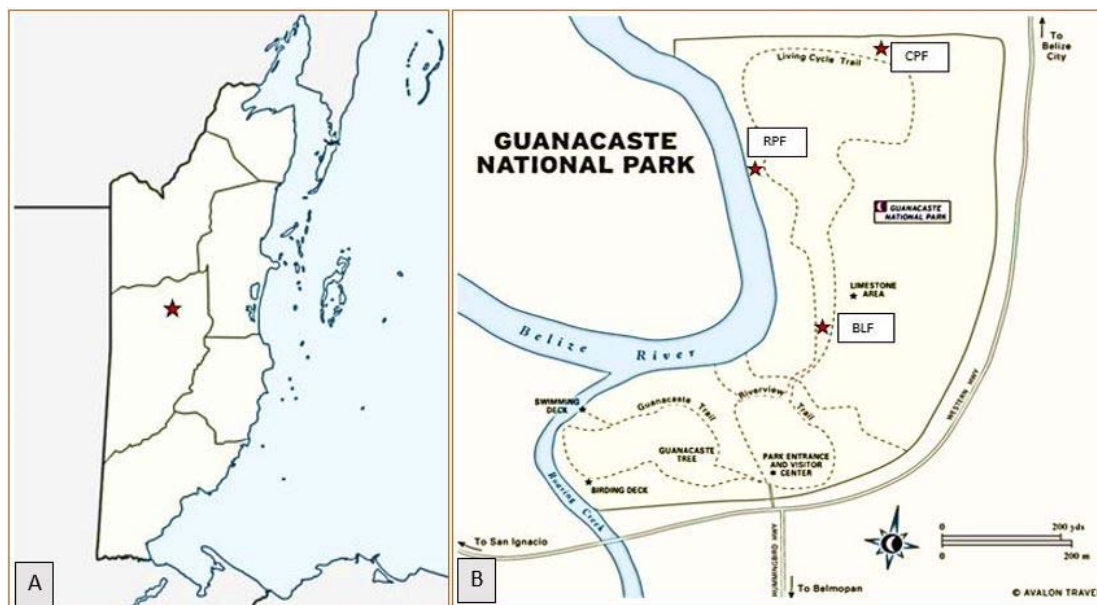


Fig 1: (A) Map of Belize showing Guanacaste National Park; (B) Map of Guanacaste National Park showing collection sites: Broadleaf forest (BLF); Cohune palm forest (CPF); Riparian forest (RPF).

It was established as a Crown Reserve in 1973 and freehold was given to Belize Audubon Society under the condition that the site be managed as a bird sanctuary or national park. It gained status as a national park in 1990. GNP's forest is secondary growth, much of it recovering from former use as pasture. Most of the forest is in the middle stages of succession. There are two broad forest types in GNP: cohune palm forest and lowland broadleaf forest. Within the lowland broadleaf forest is the riparian gallery forest along the edge of the Belize River with tree species such as provision tree (*Pachira aquatic*) and spiny bamboo (*Bambusa bambos*) and adapted to periodic flooding that occurs on the flood plain [22]. The protected area supports a small population of mammals such as nine-banded armadillo (*Dasyus novemcinctus*), gibnut (*Agouti paca*), agouti (*Dasyprocta punctata*), four-eyed opossum (*Philander opossum*), coatimundi (*Nasua narica*), howler monkey (*Alouatta pigra*), kinkajou (*Potos flavus*), and Mexican porcupine (*Coendou mexicanus*).

The national park represent an isolated forest fragment surrounded by anthropogenic developments. The closest protected forest in the region is St. Herman's Blue Hole National Park with an area of 574.5 acres (233 ha), located 12

miles on the Hummingbird Highway southwest of Belmopan City and Rio Bravo Conservation and Management Area (RBCMA) with an area of 259,206 acres (104,897ha) located 68.35 miles northeast of GNP. Belmopan city is the largest adjacent settlement with an estimated population of approximately 14,000 [23]. Just west of GNP is the village of Roaring Creek with approximately 2000 residents [23]. A number of refugee settlements (Salvapan and Las Flores) have established in the vicinity of Belmopan. These communities have grown significantly over the past 10 to 12 years. The national park's proximity to these communities and the larger population centers of Belmopan and Roaring Creek have contributed to increasing demands and pressures on the protected area with increased hunting and fishing incursions, and security issues in recent years [22].

2.2 Specimen collection

Dung beetles were collected using baited pit fall traps in the months of February, May and August in 2010. Traps were placed in 150 m transects in the three forest types (lowland broadleaf, cohune palm and riparian forests) of GNP (Fig.2).



Fig 2: Study sites at Guanacaste National Park: (A) Broadleaf forest; (B) Cohune palm forest; (C) Riparian forest

The transect in each forest type consisted of five traps spaced at a distance of 30 m. Traps consisted of plastic tubs (20x8cm) buried to its rim in soil holding a mixture of mild detergent and salt or coolant to preserve the dung beetles. A plastic sheet (33x40cm) supported by 30 cm sticks was set over each trap to restrict desiccation on warm days and flooding on rainy days. Traps were baited with horse dung or rotten meat, as most species of Scarabaeinae utilize different types of dung or rotting material [24]. Existing trails were used to reach the different forest types and traps were laid well inside the representative forest patches. For every collection effort trap contents were collected three times for the week – first after 72hrs and the subsequent two collections after 48 hrs. Each time traps were re-baited with fresh bait of the same type (horse dung or rotten meat).

The traps were emptied into fine nylon gauze (0.5 mm mesh size) to concentrate the catches from the traps. An ethanol filled wash bottle was used to wash the catch into labeled bottles. Collected beetles were identified to species level. Dung beetles < 10mm were labeled as small and ≥ 10 mm were labeled as large beetles [25]. The beetle species were designated into their functional guild (tunneler, roller and dweller) [26].

2.3 Data analysis

For the purpose of data analysis, the three collections done during a week was combined. The overall data was obtained by pooling the three monthly collections (n=45). One Way ANOVA was used to compare overall dung beetle abundance with size (<10mm vs ≥ 10 mm); functional guild (rollers, tunnelers, dwellers) and between vegetation types (lowland broadleaf forest, cohune palm forest and riparian forest). Differences with a p-value <0.05 was compared using Tukey HSD. All statistical analysis was done using SPSS 21 [27].

Pattern in species composition of dung beetle assemblage was analyzed using rank-abundance plot [28]. Species accumulation curve was drawn to determine sampling effort and the possibility of finding additional species using Estimate S (Version. 9.1.0) [29].

3. Results and discussions

3.1. Abundance and species richness

The present study showed that dung beetle community structure was negatively impacted by fragmentation and isolation. A total of 169 beetles belonging to nine genera and 15 species were collected from GNP (Table 1). Dung beetle abundance and species richness was low in GNP. The species accumulation curve for dung beetle species obtained during collection in GNP reached an asymptote and hence indicate sampling sufficiency (Fig.3).

Table 1: Dung beetle species of Guanacaste National Park, Belize. @ Beetle size (S=small, L=large); *Functional guild (T=tunneler, R=roller, D=dweller)

Species	Mean±SD	Percentage (%)	@Size	*Functional guild
<i>Ateuchus candezei</i>	0.04±0.00	1.2	S	T
<i>Ateuchus laetitiae</i>	0.44±0.99	11.8	S	T
<i>Canthon cyanellus cyanellus</i>	1.64±3.78	43.8	S	R
<i>Canthon morsei</i>	0.02±0.15	0.6	S	R
<i>Copris laeviceps</i>	0.22±0.42	5.9	L	T
<i>Coprophanæus telamon corythus</i>	0.11±0.38	3.0	L	T
<i>Deltochilum lobipes</i>	0.02±0.15	0.6	L	R
<i>Deltochilum pseudoparile</i>	0.62±1.27	16.6	L	R
<i>Dichotomius agenor</i>	0.16±0.42	4.1	L	T
<i>Eurystemus caribaeus</i>	0.09±0.29	2.4	L	D
<i>Onthophagus coscineus</i>	0.07±0.25	1.8	S	T
<i>Onthophagus crinitus</i>	0.04±0.21	1.2	S	T
<i>Onthophagus sharpi</i>	0.07±0.25	1.8	S	T
<i>Onthophagus yucatanus</i>	0.16±0.56	4.1	S	T
<i>Uroxys microcularis</i>	0.04±0.21	1.2	S	T

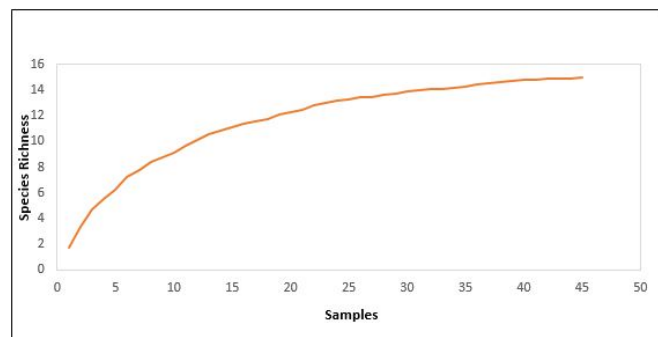


Fig 3: Species accumulation curve for dung beetles of Guanacaste National Park, Belize

Across fragmentation studies, dung beetle species richness and abundance declined in small forest fragments [30-33]. There are several possible reasons attributed to this decrease in dung beetle abundance and species richness in GNP. Studies have shown that smaller and more isolated forest remnants sustain fewer species than larger and less isolated sites since isolation affects movement and dispersal of dung beetle species and lead to high local extinction rate [30, 31, 34, 35]. If the deforested matrix surrounding the forest fragment is inhospitable to forest species, there will be little or no migration of individuals through the matrix to colonize isolated forest [36]. This is evidenced by the large number of infrequently captured species—species captured less than ten times [37] in GNP. Eleven of the 15 species collected belong to this category. They are *Ateuchus candezei*, *Canthon morsei*, *Coprophanæus telamon corythus*, *Deltochilum lobipes*, *Dichotomius agenor*, *Eurystemus caribaeus*, *Onthophagus coscineus*, *O. crinitus*, *O. sharpi*, *O. yucatanus*, and *Uroxys microcularis*. The

national park is surrounded by human habitations and modified landscapes which acts as dispersal barrier and restricts colonization by dung beetle species. As a result population will fall below viable levels and extinctions can follow [36].

Edge effect is another factor that influence richness and abundance of forest dung beetle species [38, 39]. Forest edges have a relatively higher temperature, lower humidity and is exposed to higher solar radiation when compared to forest interior and this impact organisms [40, 41]. As the fragment size decreases, edge effect becomes more pronounced [36]. This is probably another factor that affected the dung beetle species richness and abundance in the national park as GNP is a forest fragment of relatively small size.

The level of food resource available to dung beetles is also an important factor that affect the species richness and abundance. This is directly related to the general abundance of mammals in a habitat [26]. The mammals observed in GNP were all small mammals and their abundance was relatively low as observed by us during our various visits to the park and the wardens who do daily patrols through the park. The non-flying mammals such as those present in GNP are strongly sensitive to forest loss, fragmentation and isolation [11, 30, 42]. The human modified landscape that surrounds the national park acts as dispersal barriers to these mammals. Further with proximity of park to human settlements intrusion of villagers for fishing and illegal hunting and intrusion of dogs from neighboring communities have become a serious threat to many of these small mammals.

3.2. Beetle size and guild structure

Small beetles accounted for 67% of the assemblage and large beetles 33% ($F=6.46, df=1, p>0.05$) (Fig. 4). Studies have shown that large beetles are negatively impacted by fragmentation [30, 43]. This is probably due to the fact that large beetles require greater food resource and have low reproductive rate when compared to small beetles [44]. Since large beetles are more efficient in dung removal than small beetles [43, 45] the low abundance of large beetles in the park will affect the ecosystem functions such as nutrient recycling and secondary seed dispersal.

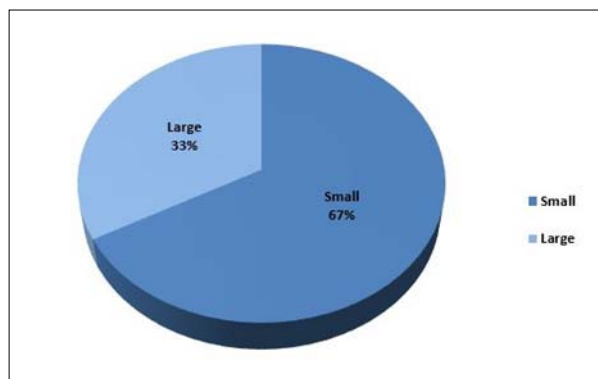


Fig 4: Proportion of small and large dung beetles in Guanacaste National Park, Belize

Functional guild abundance showed significant variation ($F = 10.39, df = 2, p<0.05$) (Table 2). Roller guild was the most abundant functional guild (62%) and it was represented by four species. Tunneler guild (36%) was represented by ten species and dweller guild (2%) by one species (Fig.5; Table1).

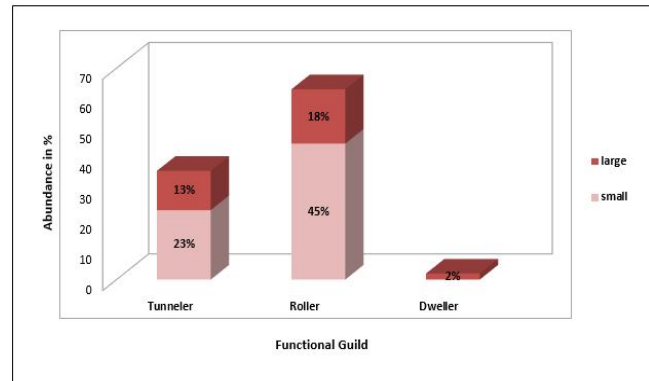


Fig 5: Functional guild composition of dung beetle species of Guanacaste National Park, Belize

Table 2: Pairwise comparison of functional guilds of dung beetles of Guanacaste National Park, Belize

(I) guild	(J) guild	Std. Error	Sig.	95% Confidence Interval	
				Lower Bound	Upper Bound
Tunneler	Roller	.10028	.000	-.6822	-.2111
	Dweller	.17777	.969	-.3754	.4598
Roller	Tunneler	.10028	.000	.2111	.6822
	Dweller	.18951	.027	.0437	.9340
Dweller	Tunneler	.17777	.969	-.4598	.3754
	Roller	.18951	.027	-.9340	-.0437

Tunnelers dominates neotropical forest dung beetle assemblages [26, 46] but in habitats with anthropogenic disturbance and modifications an increase in roller dung beetles have been observed in previous studies [47]. This trend is seen in the forest of GNP. The abundance of the roller guild was contributed chiefly by the dominant small roller *Canthon cyanellus cyanellus*, which is a eurytopic species and accounted for 43.8% of the assemblage.

Dung beetle abundance between forest types did not vary significantly ($F=2.098, df=2, p>0.05$). The three vegetation types (lowland broadleaf forest, cohune palm forest and riparian forest) found in the national park are represented by small patches intermixed and in close proximity to each other and the beetles are able to move freely between the patches and hence no difference was found in the dung beetle assemblage between the forest types of the national park.

3.3 Species composition

Small roller *C. cyanellus cyanellus* was the most abundant species. *C. cyanellus cyanellus* along with *Deltochilum pseudoparile* and *Ateuchus laetitiae* made up 72.2% of the dung beetle assemblage (Fig 6; Table 1).

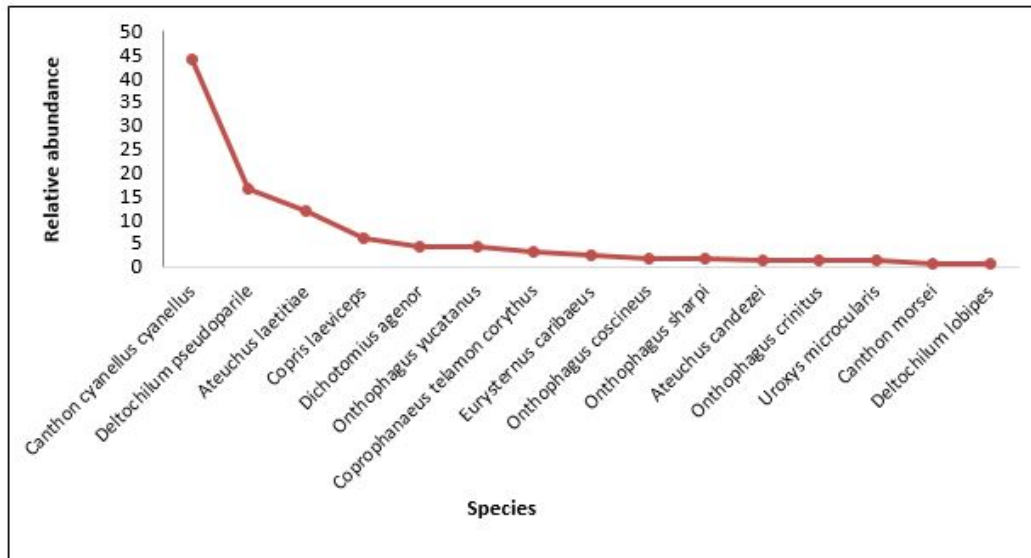


Fig. 6: Rank abundance plot of dung beetle species of Guanacaste National Park, Belize

Canthon cyanellus cyanellus, which is a eurytopic species exhibits a relatively wide range of habitat occupancy in tropical fragmented landscapes [26, 47, 48]. They are found in well preserved forests and their abundance was also found to increase in habitats with high sunlight exposure and limited tree coverage [46, 47]. This species was found to preferably use places with arboreal coverage, although they are also able to move through areas without coverage, by using small remnants of forest, or forest edge [48]. Such dung beetle species can easily migrate and establish in an isolated forest fragment like GNP and this characteristic of *C. cyanellus cyanellus* must have led to their high abundance in GNP.

4. Conclusions

Fragmentation and isolation of forest affected the dung beetle community structure of GNP negatively. This was manifested by the low abundance and low species richness of dung beetle community of the national park. The dominance of *Canthon cyanellus cyanellus*, a resilient generalist species in the protected forest is also a clear indication of the negative impact of fragmentation and isolation. The recent spate in forest clearance outside of protected area and its conversion into large tracts of agriculture land in Belize should be done with caution as it can negatively impact biodiversity in these remaining forest patches through isolation and fragmentation. Furthermore there is great need to document the biodiversity especially that of insects in Belize as this will assist in understanding the biological richness of a given area and help plan protection measures as some of these organisms could disappear even before they are documented.

5. Acknowledgements

We wish to thank the University of Belize for providing the necessary facilities to do the research and Forest Department of Belize and Audubon Society for granting permission for the collection effort. We acknowledge the assistance rendered by the wardens of Guanacaste National Park and Belize Zoo personnel during collection effort. We extend our sincere gratitude to Rolando Caballero for all the assistance and support rendered with the use of lab and its facilities; Sherlene

Enriquez-Savory, Thippi Thiagarajan, Jair Valladarez for advice and help with statistical analysis.

6. References

1. Campos RC, Hernández MIM. Changes in the dynamics of functional groups in communities of dung beetles in Atlantic forest fragments adjacent to transgenic maize crops. *Ecological Indicators*, 2015; 49:216-227.
2. Wilcove DS, McLellan CH, Dobson AP. Habitat fragmentation in the temperate zone. M.E. Soulé, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts, USA, 1986, 237-256.
3. Didham RK. *Ecological Consequences of Habitat Fragmentation*. eLS. John Wiley & Sons Ltd., 2010.
4. Didham R, Ghazoul J, Stork N, Davis A. Insects in fragmented forests: a functional approach. *Trends in Ecology and Evolution*, 1996; 11:255-260.
5. Braga RF, Korasaki V, Andresen E, Louzada J. Dung beetle community and functions along a habitat-disturbance gradient in the Amazon: A rapid assessment of ecological functions associated to biodiversity. *PLoS ONE* 2013; 8(2):e57786.
6. Souza DM, Teixeira RFM, Ostermann OP. Assessing biodiversity loss due to land use with lifecycle assessment: Are we there yet? *Global Change Biology*, 2015; 21:32-47.
7. CATHALAC. Final report: Central American land cover and land use map-land cover and land use change 1980-1990-2000-2010. Regional Program for the Reduction of Vulnerability and Environmental Degradation/CATHALAC. Panama City, Panama, 2011, 160.
8. Cherrington EA, Ek E, Cho P, Howell BF, Hernandez BE, Anderson ER *et al.* Forest cover and deforestation in Belize: 1980-2010. Technical report. Water center for the Humid Tropics of Latin America and the Caribbean/NASA/ Belize Ministry of Natural Resources and the Environment. Panama City, Panama, 2010, 42.

9. Cherrington EA, Cho PP, Waight I, Santos TY, Escalante AE, Nabet J *et al.* Executive summary: Forest cover and deforestation in Belize, 2010-2012.
10. Young C. Belize's Ecosystems: Threats and challenges to conservation in Belize. *Tropical Conservation Science*. 2008; 1(1):18-33.
11. Lovejoy TE, Bierregaard Jr. RO, Rylands AB, Malcolm JR, Quintela CE, Harper LH *et al.* Edge and other effects of isolation on Amazon forest fragments in M. E. Soul'e and B. A. Wilcox, editors. *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts, 1986, 257-285.
12. Moreno ML, Fernández MG, Molina SI, Valladares G. The role of small woodland remnants on ground dwelling insect conservation in Chaco Serrano, Central Argentina. *Journal of Insect Science*. 2013; 13:40.
13. Bang HS, Lee J-H, Kwon OS, Na YE, Jang YS, Kim WH. Effects of paracoprid dung beetles (Coleoptera: Scarabaeidae) on the growth of pasture herbage and on the underlying soil. *Applied Soil Ecology*. 2005; 29:165-171.
14. Losey JE, Vaughan M. The economic value of ecological services provided by insects. *Bioscience*, 2006; 56:311-323.
15. Andresen E, Levey DJ. Effects of dung and seed size on secondary dispersal, seed predation, and seedling establishment of rain forest trees. *Oecologia*, 2004; 139: 45-54.
16. Hingston RWG. *A Naturalist in Hindustan*. H.F. and G. Witherby, London, 1923.
17. Favila M, Halffter G. Indicator groups for measuring biodiversity. *Acta Zoológica Mexicana (n.s.)* 1997; 72:1-25.
18. Shahabuddin Hasanah U, Eljonnahdi. Effectiveness of dung beetles as bioindicators of environmental changes in land-use gradient in Sulawesi, Indonesia. *Biotropia*. 2013; 21:1, 20114:48-58.
19. Viegas G, Stenert C, Schulz UH, Maltchik L. Dung beetle communities as biological indicators of riparian forest widths in southern Brazil. *Ecological Indicators*, 2014; 36:703-710.
20. Halffter G, Edmonds WD. The nesting behaviour of dung beetles (Scarabaeinae): An ecological and evolutive approach. *Instituto de Ecología, México, DF. Man and the Biosphere Program UNESCO*, 1982, 177.
21. Cambefort I. Dung beetles in tropical savannas. Hanski I. and Cambefort I. (eds) *Dung Beetle Ecology*. Princeton University Press, New Jersey, USA, 1991, 156-178.
22. Walker Z, Walker P. *The Directory of Belize's Protected Areas*. Wildtracks, Belize, 2011, 154.
23. Statistical Institute of Belize. *Belize population and housing census country report*. www.statisticsbelize.org.bz. 2010.
24. Halffter G, Mathews EG. The natural history of dung beetles of subfamily Scarabaeinae (Coleoptera: Scarabaeidae). *Folia Entomológica Mexicana*. 1966, 1-312.
25. Barragán F, Moreno CE, Escobar F, Halffter G, Navarrete D. Negative impacts of human land use on dung beetle functional diversity. *PLoS ONE*, 2011; 6(3):e17976.
26. Hanski I, Cambefort I. *Dung beetle ecology*. Princeton University Press, USA, 1991.
27. IBM SPSS Statistics for Windows, Version 21.0. Armonk, NY, IBM Corp, 2012.
28. Whittaker RH. Dominance and diversity in land plant communities. *Science*, 1965; 147:250-260.
29. Colwell RK. Estimate S. Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application. University of Connecticut, 2013.
30. Klein BC. Effects of forest fragmentation on dung and carrion beetle communities in Central Amazonia. *Ecology*, 1989; 70:1715-1725.
31. Gill B. Dung beetles in tropical American forests. In: Hanski I. and Cambefort I. (eds) *Dung Beetle Ecology*. Princeton University Press, New Jersey, USA, 1991, 211-229.
32. Nichols E, Larsen T, Spector S, Davis A, Escobar F, Favila M *et al.* Dung beetle response to tropical forest modification and fragmentation: a quantitative review and meta-analysis. *Biological Conservation*, 2007; 137:1-19.
33. Gardner TA, Hernandez MIM, Barlow J, Peres CA. Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. *Journal of Applied Ecology*. 2008; 45:883-893.
34. Howden HF, Nealis VG. Effects of clearing in a tropical rain forest on the composition of the coprophagous scarab beetle fauna (Coleoptera). *Biotropica*, 1975; 7:77-83.
35. Peck SB, Forsyth A. Composition structure, and competitive behavior in a guild of Ecuadorian rain forest dung beetles (Coleoptera: Scarabaeidae). *Canadian Journal of Zoology*. 1982; 60:1624-1634.
36. Turner IM. Species loss in fragments of tropical rain forest: a review of evidence. *Journal of Applied Ecology*. 1996; 33:200-209.
37. Chazdon RL, Colwell RK, Denslow JS, Guariguata MR. Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of Northeastern Costa Rica. *Man and the Biosphere Series In: Dallmeier, F., Comiskey, J.A. (eds.). Forest biodiversity research, monitoring and modeling: conceptual background and old world case studies*. 1998; 20:285-309.
38. Feer F. Responses of dung beetle assemblages to characteristics of rain forest edges. *Ecotropica*, 2008; 14:49-62.
39. Díaz A, Galante E, Favila ME. The effect of the landscape matrix on the distribution of dung and carrion beetles in a fragmented tropical rain forest. *Journal of Insect Science*. 2010; 10:1-81.
40. Kapos V. Effects of isolation on the water status of forest patches in the Brazilian Amazon. *Journal of Tropical Ecology*. 1989; 5:173-185.
41. Brown N. The implications of climate and gap microclimate for seedling growth conditions in a Bornean lowland rainforest. *Journal of Tropical Ecology*. 1993; 9:153-168.
42. Estrada A, Coates-Estrada R, Anzures A, Cammarano P. Dung and carrion beetle in tropical rainforest fragments and agricultural habitats at Los Tuxtlas, Mexico. *Journal of Tropical Ecology*. 1998; 14:577-593.

43. Larsen TH, Williams NM, Kremen C. Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters*, 2005; 8(5):538-547.
44. Hernández MIM, Monteiro LR, Favila ME. The role of body size and shape in understanding competitive interactions within a community of Neotropical dung beetles. *Journal of Insect Science*. 2011; 11:13.
45. Slade EM, Mann DJ, Villanueva JF, Lewis OT. Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. *Journal of Animal Ecology*. 2007; 76:1094-1104.
46. Halfpeter G, Favila ME, Halfpeter V. A comparative study of the structure of the scarab guild in Mexican tropical rain forests and derived ecosystems. *Folia Entomológica Mexicana*, 1992; 84:131-156.
47. Navarrete D, Halfpeter G. Dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae) diversity in continuous forest, forest fragments and cattle pastures in a landscape of Chiapas, Mexico: the effects of anthropogenic changes. *Biodiversity and Conservation*, 2008; 17:2869-2898.
48. Arellano L, León-Cortés JL, Ovaskainen O. Patterns of abundance and movement in relation to landscape structure: a study of a common scarab (*Canthon cyanellus cyanellus*) in Southern Mexico. *Landscape Ecology*, 2008; 23:69-78.