DIFFERENCE IN DUNG BEETLE (Coleoptera: Scarabaeinae) ASSEMBLAGES IN DIFFERENT HABITAT TYPES AND HABITAT PATCHES WITHIN THE VERDE SUMACO FOREST, ECUADOR

by

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LAKEHEAD UNIVERSITY

THUNDER BAY, ONTARIO

2019

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An Undergraduate Thesis Submitted in

Partial Fulfillment of the Requirements for the

Degree of Honours Bachelor of Environmental Management

Faculty of Natural Resources Management

Lakehead University

2019

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Major Advisor   Second Reader

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ABSTRACT

Stachiw, J.W. 2019. Differences in dung beetle (Coleoptera: Scarabaeinae) assemblages in different habitat types and habitat patches within the Verde Sumaco forest, Ecuador.

Scarabaeinae, the dung-eating beetle subfamily, comprises keystone species that perform a host of ecological functions. They are easily surveyed and respond to habitat change, making them suitable indicators of effects of land use conversion on biodiversity. I set baited pitfall traps in mature forest, secondary forest, and chakras, traditional home gardens, in Verde Sumaco, Orellana, Ecuador. I investigated the effects of habitat type and edge type (mature forest adjacent to river, secondary forest adjacent to river, and secondary forest adjacent to open farm) on Scarabaeinae diversity. I found significant effects on dung beetle capture on both habitat type ($F_{(2, 21)} = 3.38$, $p = 0.05$) and edge type ($F_{(1, 21)} = 4.23$, $p = 0.05$). Total captures of Eurysternus beetles ($F_{(1, 12)} = 21.73$, $p = 0.001$), endocoprid species ($F_{(1, 17)} = 16.61$, $p = 0.001$), and telecoprid species ($F_{(1, 17)} = 5.37$, $p = 0.033$) were significantly greater when the edge was a transition between forest types or chakra, compared to when forest was adjacent to rivers or farms. Capture of the telecoprid group was significantly greater in secondary forest than mature forests ($F_{(1, 17)} = 13.91$, $p = 0.002$). These differences may be explained by a combination of natural history, ecological adaptation, and human influence. Alterations in dung beetle assemblage will modify the ecological functions being mediated by these keystone species. Within terrestrial entomofauna, dung beetles are proportionally the most affected taxa, with the primary driver of decline being habitat conversion. Losing the ecological functions that these species provide could have appreciable deleterious impacts on moist tropical forests.

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INTRODUCTION AND OBJECTIVES

Clearing and modifying tropical forests, often for agriculture, comprise a common influence in these biologically rich ecosystems (Laurance et al. 2013). Altering mega-diverse ecosystems and imposing new land uses have appreciable detrimental effects on biological diversity of an area (Gibson et al. 2011). Numerous studies have been conducted on the relationship between declines in vertebrate diversity and land use conversion, yet few studies are concerned with the impacts of land use changes and invertebrate diversity (Kenyon et al. 2016). Species comprising the dung beetle subfamily Scarabaeinae exhibit quick, graded, responses to tropical forest modification and fragmentation (Nichols et al. 2007; Spector & Ayzama 2003). Dung beetles are easily surveyed and perform a host of ecological functions, making them suitable for study of relationships between biodiversity and land use modification (Nichols et al. 2008).

Ecological functions are part of the complex interactions between biotic and abiotic components of an ecosystem that may provide goods and services to satisfy human needs either directly or indirectly (de Groot et al. 2002). Members of the subfamily Scarabaeinae provide important contributions to nutrient cycling (Tixier et al. 2015; Yokoyama et al. 1991), bioturbation (Manning et al. 2016; Mittal 1993), plant growth enhancement (Frank et al. 2017; Yamada et al. 2007), secondary seed dispersal (Andersen 2002; Slade et al. 2007), fly and parasite control (Bishop et al. 2005; Nichols et la. 2008; Ridsdill-Smith & Hayles 1990), and pollination (Gibernau et al. 2004; Sakai & Inoue 1999). The degradation of cellulose-rich dung, an indigestible polysaccharide

for most eukaryotes, is an essential function that dung beetles perform that allow them to carry out their ecosystem functions (Holter 2016).

The natural disturbance regime that shapes moist tropical forest structure is the death of one or more trees in canopy, creating canopy gaps (Herault & Piponiot 2018). These gaps allow for an increase in the quantity of light reaching the understory, resulting in the germination of shade-intolerant species in the low-light understory (Goulamoussene et al. 2016). This effect contributes to the maintenance of biodiversity in moist tropical forests (Herault & Piponiot 2018). Recent tropical forest exploitation, including long-term perturbations (i.e., land use conversion) and shorter-term alterations (i.e., logging operations), has led to a deviation from this natural succession pattern (Brienen et al. 2015; Nichols et al. 2007). Alterations in the natural disturbance regime of moist tropical forests will further alter the normal structure and function of the ecosystem (Sheil & Burslem 2003). Finally, the detrimental effects of local and regional land use changes on dung beetles are likely exacerbated due to subsequent declines in dung beetle food resources as mammal populations respond to habitat alterations (Frank et al. 2017; Nichols et al. 2008). Globally, the greatest threats to dung beetles are for species restricted to forests, as they are extirpated at high rates due to tropical forest loss, modification, and fragmentation (Nichols et al. 2007).

The aim of this study was to determine how Scarabaeinae diversity is impacted by land use and habitat fragmentation in the moist tropical forest surrounding the remote community of Verde Sumaco, Ecuador. To assess the effects of habitat patches on dung beetle assemblages, habitat patches were classified as either having "hard" or "soft" edges. I defined "soft" edges as those where the adjacent land features have relatively

similar forest structures (e.g., secondary forest interior and chakra), whereas "hard" edges are those where the forest structure is significantly different (e.g., secondary forest next to farms). Dung beetle captures in small, baited pitfall traps were recorded and the number of captures by genus was subdivided into functional groups (groupings of Scarabaeinae species with similar influences on ecological functions) based on nesting behaviour (i.e., paracoprid, teleocoprid, and endocroprid). Division of dung beetle data in this way is a common practice, because quantity of these functional groups within an area dictates the resource partitioning that is occurring and also how ecosystem function may be affected (Slade et al. 2007). My objectives were to investigate: (i) the degree to which habitat surrounding the community of Verde Sumaco influences Scarabaeinae diversity; and (ii) whether the habitat patches defined as having "soft edges" retain a greater diversity of dung beetles than those defined as having "hard edges." I predicted that Scarabaeinae assemblages are more diverse and dung beetles are more abundant in mature forest than in the anthropogenically-altered habitat types, and that abundance and diversity of Scarabaeinae is greater in habitat patches with soft edges than in patches with hard edges.

LITERATURE REVIEW

ECOLOGICAL FUNCTIONS OF NEOTROPICAL DUNG BEETLES

Ecological functions are natural processes (ecological processes and ecosystem structures) that are a part of the complex interactions between the biotic and abiotic components of an ecosystem. They may provide goods and services to satisfy human needs either directly or indirectly (de Groot et al. 2002). The beetle subfamily Scarabaeinae contributes to the ecological functions of nutrient cycling, bioturbation, plant growth enhancement, secondary seed dispersal, fly and parasite control, and pollination.

The behavioural ecotype involved in nesting strategy informs the contribution of a species to the broad number of ecological functions provided by members of the Scarabaeidae family (Campos & Hernandez 2015). The degradation of cellulose-rich dung, an indigestible polysaccharide for most eukaryotes, is the essential characteristic that dung beetles possess that allows them to carry out their ecosystem functions (Holter 2016). There are three broad nesting strategies within the dung beetle subfamily: paracoprid, teleocoprid, and endocroprid, or dung tunnellers, rollers, and dwellers, respectively (Hanski & Cambefort 1991; Nichols et al. 2008; Numa et al. 2012): Tunnellers dig directly below a dung deposit to construct their nest chambers; rollers detach and transport a portion of dung from the deposition site before burying it and utilizing the resources; and the life strategy of dwellers involves the creation of nest chambers within a dung deposit (Hanski & Cambefort 1991; Kenyon et al. 2016; Numa et al. 2012). A recent study by Estes et al. (2013) attributes the ability of dung beetles to

degrade cellulose-rich dung to communities of bacterial endosymbionts that each dung beetle is inoculated with in the brood chamber.

Nutrient Cycling and Plant Growth Enhancement

Often, available nitrogen is a limiting element in plant productivity and, by increasing its abundance, dung beetles enhance plant growth. The extent to which nutrients in voided vertebrate excreta are returned in a useable form to the soil and biotic nutrient cycle has implications for plant productivity (Nichols et al. 2008). Tunnelling and nesting behaviours in the paracoprid species increase the input of nutrients into the soil, providing appreciable benefits to vegetation, while telecoprid species disperse nutrients across soil (Frank et al. 2017; Tixier et al. 2015). Yamada et al. (2007) report a significant positive relationship between paracoprid dung beetle abundance and the quantity of released inorganic nitrogen and available potassium and phosphorus in the dung of large, herbivorous mammals. Paracoprid nesting behaviour enhances soil fertility via increased mineralization rates, which subsequently increases the amount of nitrogen available for plant uptake (Yokoyama et al. 1991). Mineralization rates are increased as dung beetles alter the microorganism fauna in their brood balls and in the dung pats they feed on; their tunneling activity elevates carbon and nitrogen levels in the upper soil layer, resulting in increased habitat for ammonifier bacteria colonies.

Ex situ studies report that the mixing of dung with soil by dung beetles results in significant increases in plant height (Galbiati et al. 1995), above ground biomass (Bang et al. 2005), protein levels (Macqueen & Beirne 1975), and nitrogen content (Bang et al. 2005). One *in situ* study determined that unmanipulated, higher dung beetle abundances in their natural habitat are associated with higher net primary productivity of heathland

plants (Borrghesio 1999). Dung beetles have also been found to rival chemical fertilizers in their effects on nutrient mobilization (Miranda et al. 2000), creating significantly higher agricultural or pasture yields than in the absence of dung beetles with modest fertilization application (Fincher et al. 1981).

Bioturbation

Bioturbation is the displacement and mixing of sediment by flora or fauna, which may influence the diversity of soil biota, aeration of soil, and water porosity, all of which in turn influence plant productivity (Nichols et al. 2008). The tunnelling behaviour of paracoprid beetles while constructing nesting chambers plays a role in the ecological function of bioturbation, by transferring large quantities of earth to the soil surface (Mittal 1993). The degree of soil bioturbation is positively related to dung beetle body size, as the tunnel depth and amount of soil removed are also positively related to the size of the dung beetle (Bang et al. 2005). Only dung beetles with the largest body sizes had significant positive effects on soil porosity and permeability, with no effects on these factors at soil depths greater than 10 cm.

Secondary Seed Dispersal

Seeds within mammalian dung represent a contaminant to dung beetles, as they occupy space within the brood balls and they cannot be consumed by larvae (Nichols et al. 2008). However, as described by Andresen & Feer (2005), competition for dung resources is fierce with burial happening rapidly, resulting in seeds being buried. When competition is less intense, dung beetles remove seeds before dung burial. Larger-bodied and nocturnal species of dung beetles bury a disproportionally large amount of dung,

and are consequently more important in secondary seed dispersal (Andersen 2002; Slade et al. 2007). Endocoprid dung beetles do not contribute to secondary seed dispersal, as they do not alter the location of the fecal resource they are utilizing. Paracoprid dung beetles contribute minimally to horizontal secondary seed dispersal, but significantly contribute to vertical seed dispersal, as they bury dung to create their brood balls. The probability of seed dispersal and its vertical depth depend on the presence of paracoprid dung beetles (Slade et al. 2007; Vulinec 2002), the size of the seed (Andersen & Levey 2004), and the quantity (Andersen 2002) and quality of dung (Ponce-Santizo et al. 2006).

Vertical seed dispersal can have beneficial effects on plant recruitment by reducing predation risks, as seed detection decreases with greater burial depths (Andersen 1999; Nichols et al. 2008). However, vertical seed dispersal can also be detrimental to plant recruitment, as burial depths must be shallow enough to permit germination and emergence (Andersen & Feer 2005); seedling emergence is significantly reduced for many plants at depths greater than 3 cm (Pearson et al. 2002). Andersen & Feer (2005) determined that paracoprid beetles bury most seeds at depths ranging from 1 to 5 cm; thus, the secondary burial of seeds by a dung beetle may beneficially or deleteriously impact the seed's chance of germination.

Telecoprid dung beetles provide appreciable contributions to horizontal secondary seed dispersal as a result of their food acquisition strategy, but minimally to vertical seed dispersal due to their shallow nesting chambers (Nichols et al. 2008). Horizontal secondary seed dispersal benefits seed fitness in two ways: 1) by decreasing density dependent predator or pathogen attack, and 2) by increasing the survival rate of

seedling by reducing seedling density and, therefore, intraspecific competition (Peres 1997). The probability and distance of secondary seed dispersal by telecoprid beetles is influenced by seed size (Andresen & Levey 2004), with smaller seeds being transported further and at greater rates (Nichols et al. 2008).

Fly and Parasite Control

Parasite suppression by dung beetles involves the feeding and nesting behaviours of the dung beetle controlling the abundance of dung-dispersed nematodes and protozoa, as well as dung-breeding hematophagic and detrivorous flies (Nichols et al. 2008). When dung beetles and dung-breeding flies spatially and temporally co-exist, fly survival rates decrease. The decline in fly survival is a combined result of asymmetrical competition for dung, physical damage of eggs by beetles, and increased intraspecific competition as dung is removed for brood ball formation (Nichols et al. 2008; Bishop et al. 2005; Ridsdill-Smith & Hayes 1990).

Pollination

Pollination by Neotropical dung beetles is restricted to only a few plant species of the families Araceae and Lowiaceae (Gibernau et al. 2004; Sakai & Inoue 1999). The species of Scarabaeinae that do pollinate these decay-scented flowers are obligate pollinators, and while these co-evolutionary relationships are rare, the obligate nature of this association merits conservation action (Nichols et al. 2008).

VALUE OF MONITORING DUNG BEETLES

Numerous studies have been conducted on the relationship between declines in vertebrate diversity and land conversion, yet few studies assess the impacts of land use

changes and invertebrate diversity (Kenyon et al. 2016). Choosing to use dung beetles to assess the impacts of land-use on changes on invertebrate diversity is supported by the fact that they are a keystone species in tropical forests, given their role in decomposition and nutrient cycling, secondary seed dispersal, and control of vertebrate parasites (Numa et al. 2012); without these crucial ecosystem functions provided by members of the Scarabaeinae, the ecosystems in which they reside would be drastically different.

Scarabaeinae are easily surveyed, respond to habitat change, and perform a host of ecological functions, making them suitable for studies on the relationships between biodiversity and land-use modification (Nichols et al. 2008). Dung beetles are an ideal organism to study the effects of landscape conversion, as they respond to tropical forest modification and fragmentation (Nichols et al. 2007), and are shown to exhibit quick, graded responses to both natural and anthropogenic disturbances (Spector & Ayzama 2003). Cost effectiveness and reliability of data collection are important factors to consider when choosing a species group to study. Dung beetles can be reliably caught with baited pitfall traps, which, per findings by Tyre et al. (2003), results in a relatively low level of false-negative recordings. Furthermore, Nichols & Gardner (2011) report that dung beetle sampling via baited pitfall traps is relatively insensitive to variability in study design, thus providing greater ability to compare results between studies. Finally, field work equipment and specimen processing time for dung beetle surveys are low-cost when compared to surveys of other tropical species, and the field research is more cost- and time-efficient than for many other commonly studied species groups, all the while providing a high performance as an indicator species (Figure 1; Gardner et al. 2008).
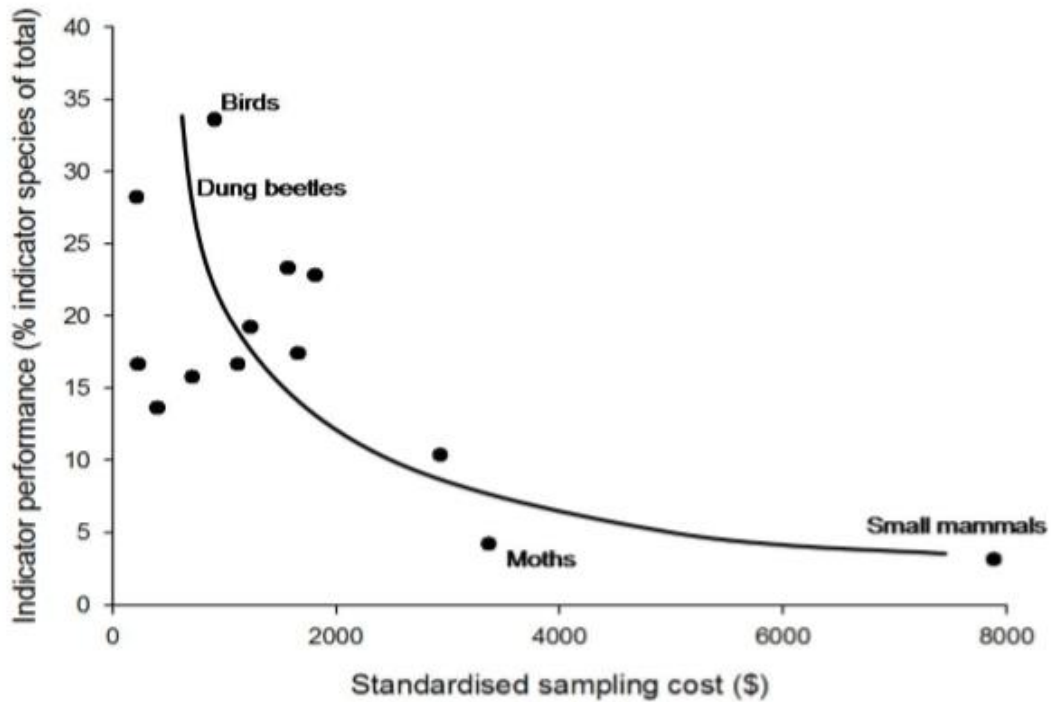
Figure 1. Comparing patterns of indicator value against standardised survey cost across 14 commonly studied Amazonian taxa (Gardner et al. 2008).

TRENDS IN DUNG BEETLE DIVERSITY

<u>Natural Trends</u>

Dung beetles are cosmopolitan, residing on every continent except Antarctica. Their highest diversity is in tropical forests and savannas (Simmons & Ridsdill-Smith 2011; Nichols et al. 2008; Halffter 1991), specifically, tropical forest and savanna biomes in Afrotropical and Oriental regions (Tarasov & Solodovnikov 2011). Glacial cycles may be responsible for differences in diversity across biogeographic regions, as over the last several million years the relative extent of forest and grasslands in Africa,

Asia and South America has differed, usually with a greater quantity of open vegetation occurring in the Afrotropical and Oriental regions than in the Neotropical region (Colinvaux et al. 2000). Consequently, fewer Neotropical dung beetle genera have evolved to fill ecological niches specific to open-formation vegetation (Scholtz et al. 2009). Glacial cycles have also resulted in Afrotropical and Oriental regions being considered a cohesive biogeographic unit significantly differing from the Neotropical biogeographic region, given shared evolutionary histories and significant faunal overlap.

Suitable climate and the variety of dung types influence the distribution of dung beetles worldwide (Davis & Scholtz 2001; Davis et al. 2002). Davis (1997) proposed that it is edaphic differences that underpin the patterns of dung beetle association with vegetation types, while Doube (1991) claimed that soil itself directly influences local Scarabaeinae assemblages and determines local population viability. The latter view is substantiated by Vessby & Wiktelius (2003), who found soil structure and consistency can directly affect reproductive site selection in dung beetles. Combining edaphic conditions and specific climate illustrates yet another pattern in the distribution of dung beetles. Dung beetles will occur and persist in a variety of habitat types, so long as they display similar soil and climate conditions (Nichols & Gardner 2011). For example, a study by Davis & Phillips (2009) showed that dung beetles inhabiting a matrix of plantation and farmland in a fragmented forest landscape on the Ivory Coast were a subset of the species that originated nearby savannah areas. Klein (1989) found that, in large tracts of contiguous mature forest, dung beetle populations are greater than in secondary forests, and that dung beetles do not cross open canopy landscapes, probably due to the potential for their desiccation.

Dung beetles are highly responsive to environmental heterogeneities across multiple scales and levels of ecological organizations, which will dictate how local dung beetle communities are assembled (Nichols & Gardner 2011). High rates of species turnover occur across neighbouring habitat types, often over very short distances (only hundreds of meters). Spector & Ayzama (2003) reported that in directly adjacent savannah and forest sites, 24 of the 50 most common species were restricted to a single vegetation type. Similarly, Davis et al. (2001) found significant differences in species compositions of dung beetle assemblages comparing adjacent riverine and interior rainforest. However, the latter investigation also showed significant deviation in Scarabaeinae assemblages at finer-scale subdivisions within forest types, with different species occupying slightly different microclimates (i.e., species assemblages were clustered in river-edge, river-bank, and riverine non-edge/bank communities). Sowig (1995) found that functional groups without the ability to relocate dung, endocoprid and paracoprid dung beetles, are relatively more sensitive to soil conditions. Reproductive success in endocoprid species also declines with high temperatures and low moisture (in open-vegetation habitats), as the drying of dung decreases its nutrient content (Numa et al. 2012).

Trends in Diversity Resulting from the Natural Availability of Dung Resources

Dung beetles utilize the fecal deposits of animals as their primary resource (Young 2015). Their natural history and their ecological specialization were hypothesized to be linked to the evolution of terrestrial vertebrates (Davis 1990), which also explains their subsequent speciation (Davis et al. 2002). However, Chin & Gill (1996) have refuted this claim, suggesting that dung beetles evolved coprophagy in

association with dinosaurs long before the ecological linkage between dung beetles and mammals was formed. Without dispute, however, both the type of dung and its quantity influence the natural distribution of Scarabaeinae species. For example, Lobo et al. (2006) found that the hydric content of dung and the density of dung deposits influence the diversity and abundance of dung beetles. Some species are found where dung with high hydric content occurs, e.g., with the dung of large mammals, while other species are found where dung with low hydric content occurs, e.g., with the dung of rabbits and deer (Verdu & Galante 2004). Variation in mouthpart adaptation is responsible for these preferences by dung type.

As a result of the feeding and breeding specialization of Scarabaeinae, they are sensitive to changes in availability of dung (Nichols et al. 2009). Evidence for this sensitivity comprises a set of studies on changes in native mammal assemblages as a result of persistent human hunting pressure and altered grazing regimes (Nichols & Gardner 2011; Andresen & Laurance 2007; Carpaneto et al. 2005). Estrada et al. (1998) found a positive relationship between terrestrial mammal richness and abundance and dung beetle species richness and abundance across a gradient of land-use intensity. Similarly, Andresen & Laurance's (2007) study across a gradient of hunting intensity found a significant negative response in dung beetle diversity with decreasing abundance of mammals.

Dung Beetle Response across Land-Use Intensification Gradients in Tropical Forests

Deviations from the natural disturbance regime in moist tropical forests alter the normal structure and function of the ecosystem (Sheil & Burslem 2003). Dung beetles are highly sensitive to the direct impacts of tropical forest conversion (Nichols et al.

2007), as well as to the indirect effects associated with changes to the availability of mammalian fecal matter (Nichols et al. 2009). Specifically, changes in local and regional-scale land use and changes in mammalian fauna abundance and diversity adversely impacts the diversity and abundance of dung beetles (Frank et al. 2017; Nichols et al. 2008). The detrimental effects of land-use changes on dung beetles are likely exacerbated due to subsequent declines in dung beetle food resources as mammal populations respond to habitat alterations. Globally, the greatest anthropogenic threats to dung beetles are to forest-dwelling species, as they are being extirpated at high rates due to tropical forest loss, modification, and fragmentation (Nichols et al. 2007). Reforested habitat, including secondary forest and plantation forests, offers low conservation value for dung beetles (Gardner et al. 2008). However, when natural forests and grasslands are converted to pasture, there is range expansion for some dung beetles, even as other species become extirpated from the area (Davis et al. 2004).

Scarabaeinae species assemblages in any land use type that offers some degree of forest cover (i.e., selectively logged forest, secondary forests, and agroforests) were shown to be similar to those found in intact tropical forests (Pineda et al. 2005). However, Nichols & Gardner (2011) report that heavily modified tropical forests (those with little to no canopy cover) have species-poor Scarabaeinae communities, with high rates of species turnover, altered abundance distribution, and significantly smaller dung beetle body sizes, when compared to the species assemblages found in intact moist tropical forests. These dramatic changes are reportedly a result of severely modified forests having higher air and soil temperature than intact forest, pushing species beyond a lethal upper temperature of approximately 42°C (Chown & Klok 2011; Verdu et al.

2006). Lower survival as a result of thermo-intolerance and enhanced emigration from modified forests are effects most pronounced for larger-bodied dung beetle species (Larsen et al. 2008; Larsen et al. 2005). Further compounding the impacts on larger-bodied species is the fact that in these degraded land-use types there are fewer feces from larger-bodied mammals, which is the preferred food type in larger beetles (Nichols et al. 2009).

The generalized decline in dung beetle species richness across the eight most common anthropogenic land uses in moist tropical forests can be shown via a box and whisker plot (Figure 2). In summary scarab diversity in anthropogenically modified tropical forests depends on the degree of forest fragmentation. Forest fragments suffer similar dung beetle community response patterns to those in any human-modified areas, as the fragments have reduced richness, abundance, and species evenness relative to
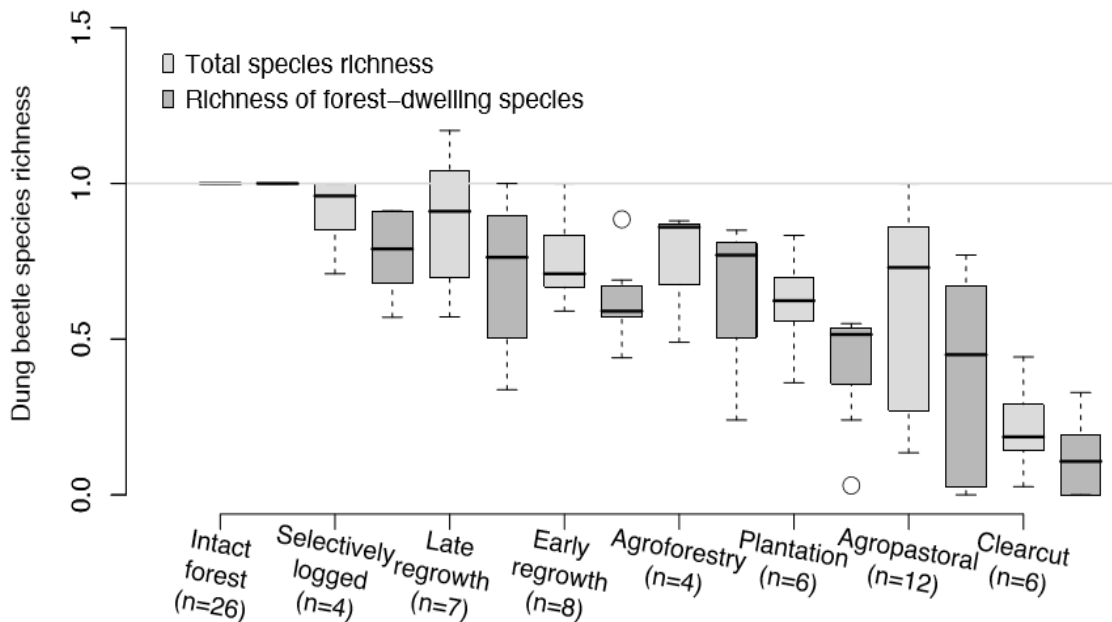
Figure 2. Generalized declines in dung beetle species richness across common anthropogenic land uses in moist, Neotropical forests. Light grey represents the total number of species in a given land-use, and dark grey illustrates the proportion of species recorded in that land-use that were also captured in the intact forest (Nichols et al. 2007).

intact forests (Nichols et al. 2007). Gardner et al. (2009) found that richness, abundance, and species evenness vary positively with forest fragment size.

Trends in Diversity Resulting from Human-Altered Availability of Dung Resources

According to Nichols (2012), declines in mammal populations will impact dung beetles by lowering the diversity of available dung types, shifting the dominant dung type from large, moist depositions to smaller, drier, pelleted type depositions, thus directly affecting the species with obligate associations for certain dung types. Alterations in dung resource availability produces changes to dung beetle community structure (Koh et al. 2004) and ecological function (Eklof & Ebenman 2006). Peres & Palacios (2007) report significant declines in large-bodied Amazonian species, which according to Peres & Lake (2003) have occurred even in the most inaccessible regions of Amazonia. This defaunation has two potential cascading trophic effects: 1) extirpation and possible extinction of the dung beetles, and 2) a subsequent decline in the ecological processes they provide (Nichols et al. 2009).

In Neotropical forests experiencing significant hunting pressure, the total biomass of large, moist dung deposits is significantly depressed, while the amount of small, dry, pelleted dung produced by rodents, armadillos and small primates increases (Peres & Palacios 2007). The implications of this anthropologically-driven dung resource shift depends on the level of resource use plasticity in a beetle species and the relationship between dung availability and its population fitness (Nichols et al. 2009). While most scarab species are generalists, capable of feeding on dung from multiple species, there are studies which have found that even these generalists discriminate

between dung type, its hydric content, its nutritional value, and its shape (Verdu &

Galante 2004; Chame 2003).

MATERIALS AND METHODS

STUDY AREA

This study was conducted near and within the Sumaco Biosphere Reserve

(00°32'S, 77°23'W), an area classified as a biodiversity hotspot in the Amazon region of

the Ecuadorian tropical Andes (UNESCO 2011; Myers et al. 2000). Sampling occurred

in forest surrounding the remote Kichwa community of Verde Sumaco, Ecuador, ca. 10

km from the nearest trafficable road in the town of Loreto, Ecuador (Oldekop et al.

2013). The traditional territory of this community spans 24,734 ha, including an area of

forest reserve (18,546 ha) that encompasses 90% of its landbase. The community is at an

elevation of 324 m.a.s.l. and constitutes about 290 residents (Torres 2018).

DUNG BEETLE COLLECTION

Sampling took place in December 2017 within a radius of 5 km from the

community. All sample sites were classified as moist tropical forest (Pearman 1997).

Beetles were captured in three different habitat types and three defined habitat patches.

Habitat types included *chakra* (agroforest) interior, mature forest interior, and secondary

forest interior, and the habitat patches were defined by the adjacent habitat: open farm,

river edge, or secondary forest. Habitat patches with a relatively similar forest structure

adjacent to them (e.g., secondary forest interior and mature forest) were classified as

having "soft" edges, whereas "hard" edges were those where the adjacent area was

significantly different from the habitat type studied (e.g., secondary forest interior next to open farm).

Baited pitfall traps were implemented to collect specimens, with the transect design relying on recommendations by Larsen & Forsyth (2005). Their standardized dung beetle transect approach satisfies the requirements of adequate sample size, allows easy placement at any site, and minimizes trap interference. Fifteen pitfall traps were placed in each transect. Traps consisted of plastic containers 15 cm high and 10 cm in diameter. Each trap was filled to about half capacity with soapy water, then buried at ground level. Above each trap, 50 g of pig faeces, spoiled beef, or rotten banana stock was placed within a square of fine mesh and suspended ca. 5 cm above the center of the trap. Trap transects were established with a 50-m spacing between traps and five replicates of each bait type alternating along the transect. Interior transects were located 500 m from the edge of each habitat patch, while additional transects were located 50 m from the edge to test the influence of the differing edge types. Five transects were established in each of the habitat and edge types. Traps were set between 8:00 h and 12:00 h and dung beetles were collected 24 hours later.

Once collected, beetles were classified into Operational Taxonomic Units (OTUs) based on morphotype. Total capture of each OTU was determined by sampling night and transect. Voucher specimens of all morphotypes were sent for identification to Dr. Carlos Carpio, Faculty of Natural Resources, Escuela Superior Politécnica de Chimborazo (ESPOCH) Riobamba, Ecuador. Dr. Carpio was able to identify each morphotype to genus.

DATA ANALYSIS

Dung beetle capture data were examined both by genus and functional group based on nesting behaviour: paracoprid, endocoprid, and telecoprid. Six of eleven genera captured each comprised less than 3% of the total capture, so in all general linear models by genus, the captures for these genera were combined and categorized as "Other" (a total of 7.4% of captures). Similarly, there were only 9 and 7 beetles captured in two transects, and no beetles caught in another two transects; data from these four transects was removed from the final dataset. These outliers were in secondary forest in a collection period with heavy rains.

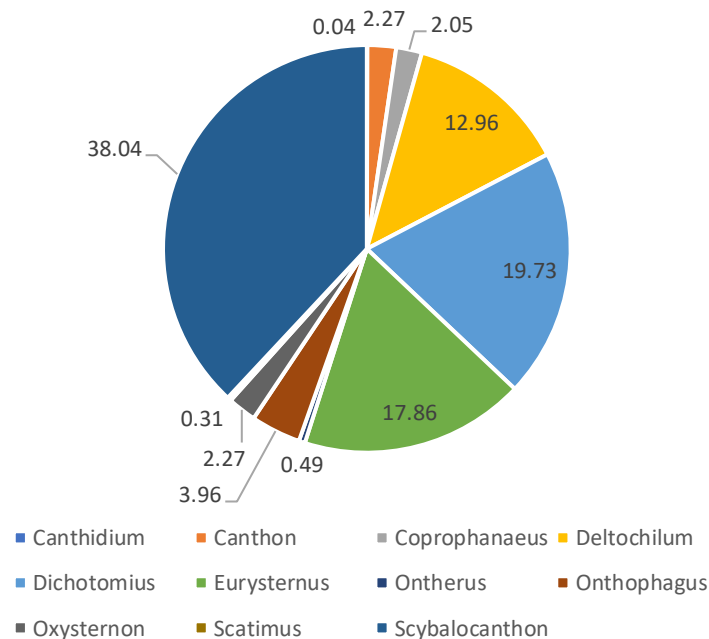Figure 3. The contribution (in percentage) of each captured genus to the total dung beetle capture.

Data was analyzed using SPSS first to provide descriptive statistics. Analyses of variance (ANOVAs) were performed to assess variance amongst richness and evenness in the captures across habitat and edge types, first calculating these measures using genus, and second using functional group (for evenness only). Richness was the number

of genera in the captures. Evenness was calculated with Shannon's diversity index

(Gorelick 2006), $H = -\sum_{i=1}^{m} p_i * \ln(p_i)$, where p_i is the proportion of species i relative

to the total richness, multiplied by the natural logarithm ($\ln p_i$), with the resulting product

summed across species, and multiplied by the inverse. Multivariate analyses of variance

(MANOVAs) were also used to assess the influence of edge type and habitat type on the

abundance by genus, excluding the *chakra* habitat type which, on preliminary

examination of the capture data, was too similar to the adjacent secondary forest. A

correspondence analysis using symmetrical normalization was generated for

visualization of relationships between genera, habitat type, edge type, and adjacent

habitat in a multidimensional space.

RESULTS

A total of 2,248 specimens in 11 genera, were captured (Table 1, Figure 3).

Paracoprid species were most common, comprising 50.9% of the total catch, 31.2%

were telecoprid, and 17.8% were endocoprid. A majority (68.1%) of the captures were in

Table 1. Total number of each species captured in mature forest interior (MFI), mature forest adjacent to river (MFR), chakra (CHK), secondary forest interior (SFI), secondary forest adjacent to river (SFR), and secondary forest adjacent to farm (SFF).

Species	MFI	MFR	CHK	SFI	SFR	SFF	Total
Canthidium sp. 1	0	0	0	1	0	0	1
Canthon sp. 1	15	2	8	17	7	2	51
Coprophanaeus sp. 1	16	16	4	3	10	0	49
Deltochilum carinatum	4	0	3	3	2	0	12
Deltochilum oberbengeri	77	49	27	28	22	31	234
Deltochilum sp. 1	19	6	3	8	8	1	45
Dichotomius sp. 1	6	3	13	12	11	8	53
Dichotomius sp. 10	3	0	1	1	0	1	6
Dichotomius sp. 2	0	1	4	2	0	0	7
Dichotomius sp. 3	21	66	46	43	20	47	243
Dichotomius sp. 4	6	6	22	12	4	4	54
Dichotomius sp. 5	2	1	0	0	1	2	6
Dichotomius sp. 6	0	0	0	0	0	1	1
Dichotomius sp. 7	0	0	2	0	0	0	2
Dichotomius sp. 8	7	19	6	8	18	5	63
Dichotomius sp. 9	1	1	0	0	6	0	8
Eurysternus sp. 1	93	17	24	47	25	3	209
Eurysternus sp. 2	32	29	30	52	31	18	192
Ontherus sp. 1	0	5	2	0	1	0	8
Ontherus sp. 2	1	1	0	1	0	0	3
Onthophagus sp. 1	11	0	3	10	8	1	33
Onthophagus sp. 2	6	4	5	11	15	1	42
Onthophagus sp. 3	0	1	3	1	3	0	8
Onthophagus sp. 4	3	0	0	0	1	0	4
Onthophagus sp. 5	0	0	0	1	0	1	2
Oxysternon sp. 1	10	10	13	8	7	3	51
Scatimus sp. 1	0	2	1	1	1	2	7
Scybalocanthon sp. 1	0	0	25	0	15	0	40
Scybalocanthon sp. 2	29	28	199	332	105	121	814
Total	362	267	444	602	321	252	2248

traps baited with feces, 30.6% were in traps baited with spoiled beef, and only 1.3% were in traps baited with rotten banana stock. No genus displayed an exclusive relationship with any one bait type.

SCARABAEINAE RESPONSE TO HABITAT TYPE AND HABITAT PATCHES

Both habitat type ($F_{(2, 21)}$ = 3.38, p = 0.05) and edge type ($F_{(1, 21)}$ = 4.23, p = 0.05) had significant effects on total capture (Figure 4). However, these factors did not have an effect on species evenness: habitat type ($F_{(2, 21)}$ = 1.48, p = 0.25); edge type ($F_{(1, 21)}$ = 0.141, p = 0.71). There was a much greater capture where soft edges were sampled (104, SEM = 13) compared to hard edges (68, SEM = 14). Also, there was a greater capture of beetles in secondary forest (116, SEM = 15) than in mature forest (63, SEM = 15); *chakra* capture (89, SEM = 21) did not differ from that in secondary forest or mature
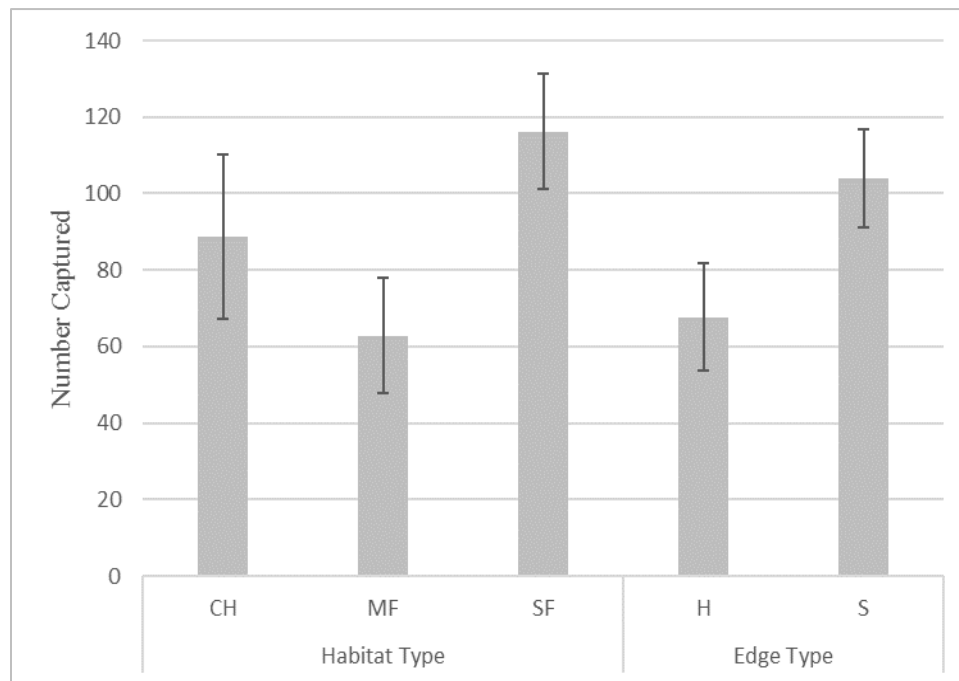

Figure 4. Total dung beetle capture by habitat type (CH = *chakra*, MF = mature forest, SF = secondary forest) and edge type (H = hard, S = soft; see text for definition).

forest. No individual genus responded significantly to habitat type ($F_{(6,7)}$ = 2.49, p = 0.129; Wilk's Λ = 0.319).

Differences in capture by functional group occurred between habitat type ($F_{(3, 15)}$ = 4.88, p = 0.015; Wilk's Λ = 0.093) and edge type ($F_{(3, 15)}$ = 14.13, p = 0.001; Wilk's Λ = 0.51). Total capture of Eurysternus beetles was greater ($F_{(1, 12)}$ = 21.73, p = 0.001) with soft edges (Figure 5). Habitat type had a significant effect on capture of telecoprid beetles ($F_{(1, 17)}$ = 13.91, p = 0.002), with a greater capture in secondary forest than mature forests, but it did not have an effect on endocoprid beetles ($F_{(1, 17)}$ = 0.046, p = 0.83) or paracoprid beetles ($F(1, 17)$ = 0.88, p = 0.36; Figure 5). Edge type had a significant effect on the capture of both endocoprid ($F_{(1, 17)}$ = 16.61, p = 0.001) and
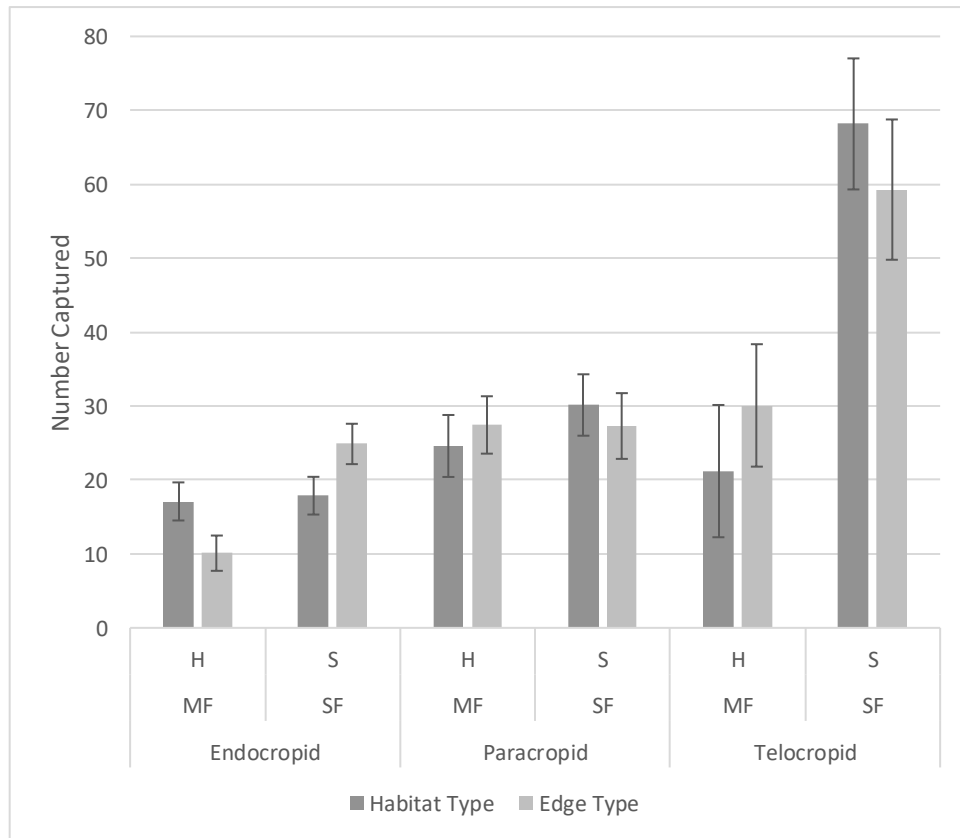

Figure 5. Mean capture by functional group against habitat type (MF = mature forest, SF = secondary forest) and edge type (H = hard, S = soft; see text for definition).

telecoprid beetles ($F_{(1,\ 17)}$ = 5.37, p = 0.033; Figure 6), with both functional groups

having a greater capture at soft edges type (Figure 4). Edge type had no significant effect

on paracoprid dung beetles ($F_{(1,\ 17)}$ = 0.001), p = 0.98).
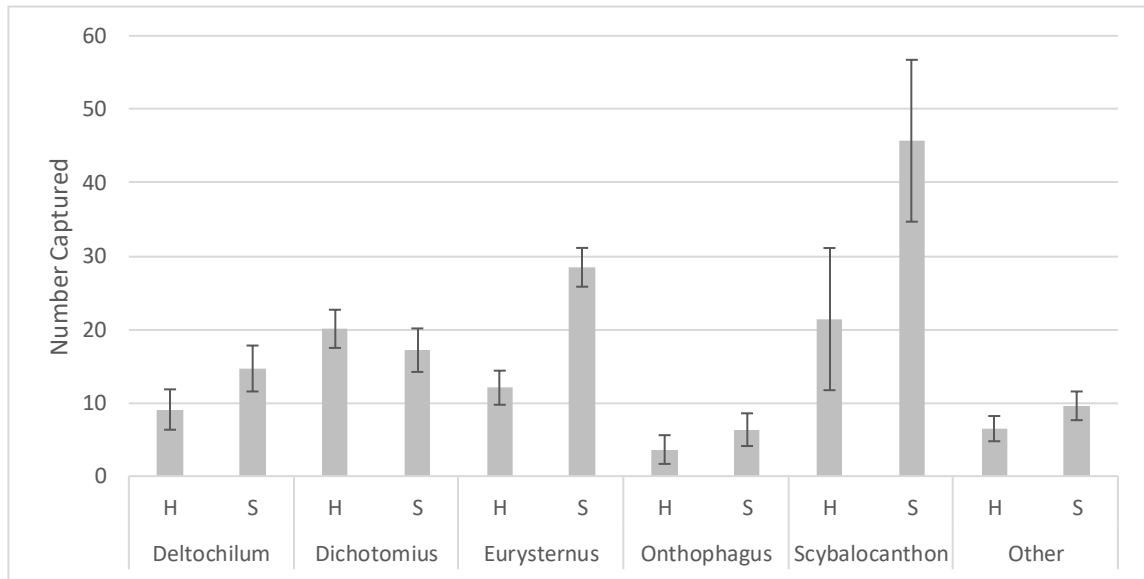
Figure 6. Mean capture by genus against edge type (H = hard, S = soft; see text for definition).

Correspondence analysis of genera (total capture) and habitat classification

(habitat type, patch types, and adjacent habitats) explained 96.6% of the variance in the

first two dimensions, and 81.3% of this variance is explained by the first dimension

(Figure 7). The ordination indicates clusters of genera along a gradient of disturbance.

Three genera (*Coprophaneus*, *Deltochilum*, and *Ontherus*) are associated with mature

forest, while *Canthidum* and *Scybalocanthon* are associated *chakra* and secondary

forest. *Dichotomius* is associated with hard edges, and *Scatimus* with soft edges.
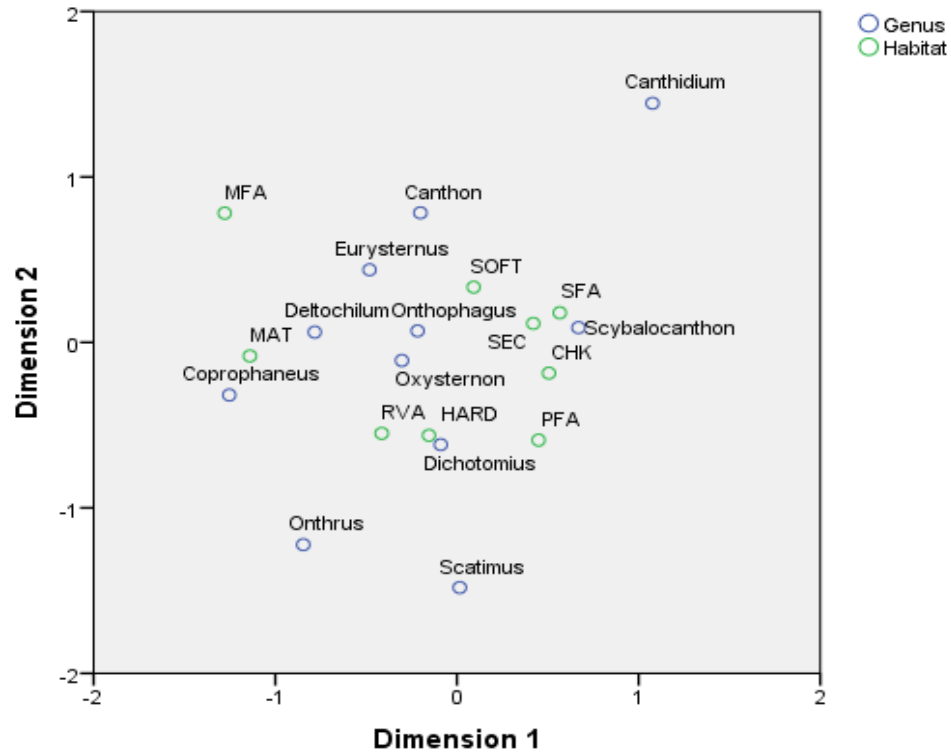
Figure 7. Correspondence Analysis ordination of genera (total capture) and habitat classification (habitat type, patch types, and adjacent habitats). Genera are indicated by blue while habitat-based variable are green.

DISCUSSION AND IMPLICATIONS

Alterations in dung beetle assemblage will modify the ecological functions they mediate (Numa et al. 2012; Slade et al. 2007), in turn altering the structure and condition of the forest (Nichols et al. 2008).In the Verde Sumaco study area, scarab assemblages were distinct in mature forest and secondary forest habitat types, as well for habitat patches with soft edges and hard edges. Differences in dung beetle abundance, both by genus and by functional group, may be explained by a combination of natural history, ecological adaptation, and human influence.

DIFFERENCES IN TOTAL ABUNDANCE

There is a positive correlation between terrestrial mammal abundance and richness, and dung beetle community richness and abundance (Andresen & Laurance 2007; Estrada et al. 1998). Significant declines in large-bodied Amazonia species can result from hunting pressure, even in the most inaccessible regions, which shifts the available dung resource type from large and moist to small and dry (Nichols 2012; Peres & Palacios 2007; Peres & Lake 2003). In large tracts of contiguous mature forest, it is commonly reported that dung beetle populations are greater than in secondary forests (Nichols & Gardner 2011; Klein 1989); however, the results for Verde Sumaco do not follow this trend. The collection of scarabs in mature forest occurred in close proximity to the community, where hunting pressure on large-bodied mammals would be appreciable. If the community of Verde Sumaco is hunting in the proximate mature forest reserve to an extent that there are inadequate large, moist dung resources to support a full complement of Scarabaeinae, there is a possibility that this defaunation, which I could not detect, could lead to two possible local trophic cascading effects: 1) extirpation and possible extinction of dung beetles that are obligate to large, moist dung resources, and 2) a subsequent decline in the ecological functions mediated by these extirpated species (Nichols et al. 2009).

Open-formation habitats have little canopy cover, leading to higher air and soil temperatures than intact forest, which pushes dung beetle species toward desiccation and decreased survival, as their body temperature reaches its upper lethal temperature (Chown & Klok 2011; Verdu et al. 2006). These conditions are also created when forest is converted to a sparsely treed land use, and may explain the lower capture of dung

beetles in Verde Sumaco in the transects along edges of secondary forest adjacent to open farm habitat, compared to any of the transects in habitat patches that had softer edges (secondary forest interior, for example). Barrier effects on immigration may also contribute to the lower capture in hard edges (secondary forest adjacent to farm and river edges, and mature forest adjacent to river edges. This interpretation reflects Klein's (1989) observations of the barrier effect on dung beetle immigration across open-formation habitats. My study also highlights the influence that hard edges have on dung beetle assemblages relative to areas in the interior of habitat patches, so long as these patches have appreciable forest structure, including in the *chakra* agroforest patches.

DIFFERENCES IN GENERA ANND FUNCTIONAL GROUP ABUNDANCE

The capture of *Eurysternus* was significantly lower in habitat patches with a hard edge. Similar findings may not be available for moist tropical forests as a whole, but it is likely that similar declines in *Eurysternus* are occurring at hard edges elsewhere. Widespread land use conversion is occurring at a rate >5% around the boundaries of reserves in the Neotropics (DeFries et al. 2005), creating hard edges at a corresponding rate. The creation of these hard edges and the subsequent loss of *Eurysternus* means a proportionate loss in the ecological services imparted by these endocoprid beetles (Slade et al. 2007).

Microclimate influences the presence and abundance of functional groups, as nesting success changes with varying conditions (Davis et al. 2001; Sowig 1995). Differences in the quantity of each functional group dictates the portioning and allocation of the dung resource, which affects which ecological functions are occurring and in what quantity (Slade et al. 2007). Changes to vegetation structure will alter

microclimates, specifically creating changes in light and moisture occur. Telecoprid species are less sensitive to the influences of soil and microclimate than endocoprid and paracoprid species, which cannot relocate dung resources (Nichols et al. 2008). Within the Verde Sumaco forest, telecoprid species were most common in the more recently disturbed habitat, most likely as a result of their ability to tolerate poorer local soil and microclimatic conditions presented by secondary forest. Endocoprid species are especially affected by microclimates with greater temperatures and lower moisture (e.g., open-formation habitats), as dung resource quality declines (Numa et al. 2012). The lower abundance of endocoprid scarabs where hard edges occurred in Verde Sumaco may reflect less than ideal microclimates in these habitat patches.

LARGER TRENDS

Among all terrestrial entomofauna, dung beetles are proportionally the most affected taxa in terms of observed global decline, with the primary driver of decline being habitat conversion (Sanchez-Bayo & Wyckhuys 2019). Species restricted to forest, which due to historic glaciation events in the Andes is a majority of Neotropical scarabs, are extirpated at high rates as tropical forests are modified, fragmented, and lost to agriculture (Nichols et al. 2007). In Verde Sumaco, three genera, *Coprophaneus*, *Deltochilum*, and *Ontherus*, are associated with mature forest habitat, of which *Coprophaneus* and *Ontherus* capture was novel for the area (Villamarin-Cortez 2014). Since the early 1990s, ca. 976,800 ha of wilderness – defined as biologically and ecologically intact landscapes free of human disturbance (Kormos et al. 2015) – has been lost within South America (Watson et al. 2016) and only ~9.8% of this biome is under protection (Dent 2010). Studies indicate that today there is a greater area of

secondary forest and human-degraded forest than there is mature tropical forest (e.g., Brooks et al. 2009). Multiple studies conclude secondary forests have a similar conservation value to dung beetle diversity as plantations, which is far lower than the biodiversity conservation value of mature forests (Gardner et al. 2009; Barlow et al. 2007).

The dung beetle community within the 1,600-ha reserve of La Selva, Costa Rica, was altered by the habitat loss surrounding the reserve, and the increasing isolation resulting from the land use conversion (Escobar et al. 2008). It is believed that the size of this neotropical, moist tropical forest reserve was not large enough to viably support a full complement of dung beetles, which will have dramatic cascading effects on the ecological integrity of the forest as the ecological services mediated by dung beetles decline (Escobar et al. 2008; Nichols et al. 2008). The Verde Sumaco reserve that constitutes the traditional territory of the people in the community is >11.5 times larger than La Selva and it is adjacent to the even larger Sumaco Biosphere Reserve. However, the entire network area still does not ensure the continuation of its scarab populations nor the ecological functions they facilitate. Isolation and habitat loss adjacent to reserves can deleteriously affect moist tropical forest biota. To safeguard the conservation merit of the Verde Sumaco reserve, its managers must ensure sufficient connectivity of the community forest with the rest of the Sumaco Biosphere Reserve network. To conserve dung beetle diversity, especially those species strongly associated with mature forest, and the host of ecological functions provided by diverse groups of scarabs, any loss of mature forest must decrease. This could be through a reduction in natural resource exploitation or an increase in mature forest reserve area.

FUTURE RESEARCH

Further exploration of dung beetle abundance in secondary and mature forests is required to understand the cause of the assemblage differences. Collection of cultural data regarding hunting in the Verde Sumaco reserve via interviews with local people would allow for an understanding of the mammal populations in the reserve forest adjacent to the community, and how the corresponding dung resources correlate with the dung beetle community. Establishing pitfall transects to capture scarabs in areas where local knowledge indicates there is minimal hunting pressure could be a follow-up activity. The resultant dung beetle data would further contribute to our understanding of the local taxa, which could aid in conservation efforts within the Verde Sumaco forest reserve and the greater Sumaco Biosphere reserve network.

Future *in situ* studies on the differences in the quantity of ecological functions occurring within each habitat type would provide valuable data to complement the baseline data presented by this study. Soil chemical analysis to determine the quantity of nutrient cycling (specifically organic nitrogen levels) and its resulting impact on plant growth enhancement may be difficult to achieve, as there are a multitude of influences and interactions occurring within the soil that make it difficult to assess the sole contribution of dung beetles to this ecological function. However, collecting data on dung beetle biomass in each of the habitat types would provide opportunity to assess the relative amount of nutrients cycled (Yokoyama et al. 1991). Furthermore, dung beetle biomass is an indicator of the quantity of available dung resources (Nichols 2012), which may allow for the determination of whether the low capture of scarabs in mature forests is related to a decline in mammals (Andresen & Laurance 2007; Estrada et al.

1998). Secondary seed dispersal data to quantify the occurrence of horizontal and vertical seed dispersal by scarabs would also provide valuable information.

Identification of the voucher specimens collected from this study, currently stored at Pontificia Universidad Católica del Ecuador (PUCE) in Quito, Ecuador, to species level would allow for a qualitative analysis of the differences in the quantity of ecological functions being mediated (Slade et al. 2007). With data at this taxonomic level, the relationship between body size and relative contribution to bioturbation (Bang et al. 2005; Mittal 1993), secondary seed dispersal (Andersen 2002), and the quantity of resource partitioning a species provides (e.g. nutrient cycling; Tixier et al. 2015) could be explored.

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