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Letter to the Editor

Forest fragment size effects on dung beetle communities?

In a recent article, Nichols et al. (2007) synthesized 33 separate studies on dung beetle communities in tropical rain forests. In regard to the 12 studies of forest fragmentation, the authors found only seven that compared intact, unfragmented forests to forest fragments. From these seven, the authors tentatively concluded that species richness and abundance declined as fragment size declined and that the surrounding matrix had an influential effect.

One problem confronted by Nichols et al. (2007) was the variation among study sites and methods, which can confound the results of meta-analyses. Three of the studies were conducted in the Central Amazon at the Biological Dynamics of Forest Fragments Project (BDFFP) and the authors of the original studies came to strikingly different conclusions. Species richness of dung beetles increased with fragment size in one study (Klein, 1989), yet showed no difference across fragment size in a parallel study conducted 14 years later (Quintero, 2002; Quintero and Roslin, 2005). The third study showed reduced species richness in 1-ha fragments, but no difference between 10-ha fragments and intact, unfragmented forest (Andresen, 2003). Furthermore, beetle abundances across fragment sizes behaved inconsistently among the studies. Following three suggestions of Nichols et al. (2007), we re-analyzed the data from these three studies.

First, Nichols et al. (2007) recommend using rarefaction when making species richness comparisons among variable sample sizes. We constructed species richness curves for each fragment size and continuous forest within each study using individual-based rarefaction (We rarefied by individuals rather than samples because we did not have sample-based data from the original studies, but we tested both methods using several of our own Amazonian dung beetle datasets and found no difference between rarefaction methods). After rarefaction, species richness showed no consistent relationship with fragment size across the three studies. Klein (1989) showed no difference in species accumulation between continuous forest and 10-ha fragments, although both had slightly (but not significantly) more species than 1-ha fragments at the end of sampling; however, the 1-ha fragments were accumulating species faster than 10-ha and continuous forest when sampling ended, leaving the possibility that the 1-ha accumulation curve might cross above the others with larger sample sizes. Rarefaction of Quintero's (2002) data showed 1-ha, 10-ha, 100-ha and continuous forest curves with nearly complete overlap in species accumulation. The 1-ha curve initially lagged in species accumulation through about 1500 individuals but then exceeded the 10-ha line at 2–3000 individuals (although not significantly so), as implied above for Klein's (1989) dataset. In contrast, rarefaction of Andresen's (2003) data showed a definitive increase in species richness from 1-ha to 10-ha to continuous forest. Taken together, rarefaction of these datasets offers no convincing pattern for species richness and fragment size, in contrast to the conclusion of Nichols et al. (2007) that species richness declines with fragment size.

Second, Nichols et al. (2007) suggests incorporating quantitative variables into fragment assessments. We compare three quantitative variables across fragments: number of beetles captured per trap-day, volume (proxy for biomass) captured per trap-day, and mean beetle size. None of the original researchers measured volume, but Klein (1989) and Andresen (2003) published species-specific lengths for many of their specimens. We derived a highly significant ($P = 0.0002$, $R^2 = 0.92$) volume and length formula (*estimated volume* = 0.0001743 * *beetle length*^{3}) from one of our Amazonian collections ($n = 350$) and used it to estimate volumes for each dataset. For a few species without length measurements, we assigned a mean length computed from Klein's (1989) original lengths. These corrections were necessary for 1% of Klein's (1989) individuals and 3–5% of Quintero's (2002) individuals (Since this mean could have been skewed by a few large beetles, we also assigned a median length computed from Klein's (1989) original lengths, but the resulting analyses were nearly identical, and are not presented). Mean beetle size was calculated by dividing the total volume by the total abundance of beetles for each fragment within each study.

We used linear covariance to analyze the effects of fragment size (model: *dependent variable = fragment size*, for which variation among studies was considered a random variable), enabling us to look for trends across fragment sizes but not explain differences among studies. Two of the three variables showed distinct patterns. Abundance (number of beetles per trap-day) was unrelated to fragment size ($P = 0.6$); however, volume of beetles per trap-day increased significantly with fragment size ($P = 0.05$). Furthermore, mean beetle size was significantly correlated with fragment size – i.e., smaller beetles in smaller fragments ($P = 0.01$). Our analysis of abundance variables indicated changes in dung beetle communities that were consistent across all three studies, and re-emphasize the recommendations of Nichols et al. (2007).

Third, Nichols et al. (2007) suggest examining the guild structure of dung beetle communities. We looked for patterns in guild structure by calculating the proportion of each class – tunneler, roller, and dweller – by fragment size for each study. A linear covariance analysis indicated a significant change in guild structure across studies, with the proportion of tunnelers decreasing as fragment size increased ($P = 0.02$). Consequently, the combined proportion of rollers and dwellers increased with fragment size, although separately, neither the increase in rollers nor in dwellers was statistically significant ($P > 0.5$).

In conclusion, our analyses of the three datasets from the BDFFP have demonstrated that dung beetle volume and beetle size increased in association with a change in guild structure, as forest fragment size increased. In contrast, there was no discernible change in species richness as fragment size increased nor was abundance consistently correlated with fragment size. Given that the Nichols et al. (2007) synthesis showed an increase in both species richness and abundance with fragment size, further studies are requisite. Nichols et al. (2007) stated this need explicitly, especially recommending replication at a landscape scale and incorporating quantitative variables into analyses. This is publication number 499 in the Technical Series of the BDFFP.

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