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Terrestrial macroinvertebrate fauna under logs in primary and secondary forest

Erica Hoaglund

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College of Natural Resources, University of Minnesota

ABSTRACT

Terrestrial macroinvertebrates are an important yet understudied group. They are present in all types of tropical forest and, due to their services as decomposers, are essential for the maintenance of a productive system. The purpose of this study was to determine if there were significant differences in diversity and community composition between macroinvertebrate communities in the primary versus secondary lower montane wet forest of Monteverde, Costa Rica. Macroinvertebrates were collected from under 20 logs in primary and 20 logs in secondary forest.

Primary forest had a higher diversity of macroinvertebrates (H' = 2.5) than secondary forest (H' = 2.05). Primary forest also showed greater evenness (0.84) than secondary forest (0.76). It was also found that primary forest had greater Order richness, 20 Orders among 20 logs versus 15 Orders among 20 logs in secondary forest. Secondary forest showed a greater abundance (145 individuals) than primary forest (105 individuals). These results were consistent with various studies done on aquatic macroinvertebrates and were probably due to differences in plant communities between primary and secondary forest.

RESUMEN

Los macroinvertebrados terrestres son un grupo muy importante que no ha sido estudiado en detalle. Están presentes en todos los tipos de bosque tropical y, debido a sus servicios como descomponedores, son un elemento crucial en todos los sistemas productivos. El propósito de este estudio fue determinar si existían diferencias significativas en la diversidad y composición de las comunidades de macroinvertebrados entre el bosque primario y el bosque secundario de Monteverde, Costa Rica. Se colectaron macroinvertebrados debajo de 20 maderos en el bosque primario y 20 en el bosque secundario.

Se encontró una diversidad más alta de macroinvertebrados en el bosque primario (H' = 2.5) que en el bosque secundario (H' = 2.05). El bosque primario también contenía más órdenes de macroinvertebrados: 20 órdenes en los 20 maderos en el bosque primario contra 15 órdenes en los 20 maderos en el bosque secundario. El bosque secundario mostró una abundancia más alta (145 individuos) que la que mostró el bosque primario (105 individuos). Estos resultados concuerdan con varios estudios sobre macroinvertebrados acuáticos y fueron probablemente debidos a las diferencias en la flora entre los dos tipos de comunidades.

INTRODUCTION

Differences between community composition of primary and secondary tropical forest have been fairly well documented for several tropical taxa. However, few studies have been done on terrestrial macroinvertebrate succession between these two communities.

The lack of information on terrestrial macroinvertebrates is surprising since macroinvertebrates are an important facet of both recovering and climax communities. They are some of the founding members of a recovering community and speed the process of regeneration by facilitating the process of decomposition (Wardle et al. 2004).

Also, primary and secondary forests are significantly different in plant composition, so it follows that their detritivorous communities would be different (Richards 1996).

Woody debris are crucial carbon stores for the community in any forest ecosystem; much of a forest biomass (and thus its nutrients) is stored in decomposing wood fragments (Delaney et al. 1998); Without the soil detritivores, such as macroinvertebrates and bacteria that process these debris, up to 20% of some forest biomasses would be trapped for decades, dependent on weathering for decomposition (Delaney et al. 1998). Succession would be significantly slowed, which would slow the process of recovery in a biome with many recovering ecosystems.

Terrestrial macroinvertebrate studies are somewhat sparse, while many have been done on aquatic macroinvertebrates and the succession of their communities. Studies have shown that succession in these macroinvertebrate communities usually follows similar patterns. Species richness and diversity increase significantly over time as a disturbed habitat was recolonized (Moorhead et al. 1998). Community composition changes significantly over time; for example, percentage of detritivores in the community decreases over time (Moorhead et al. 1998); with better habitat preservation within a disturbed area, i.e. a better buffer zone between development and habitat, a significant amount of species richness can be preserved (Moore et al. 2005). Finally, it was found that in Amazon basin aquatic macroinvertebrates, density increased with decreasing canopy coverage (Bojsen et al. 2003).

The findings of all these studies and the lack of data on terrestrial macroinvertebrate it was decided to study terrestrial macroinvertebrate between primary and secondary lower montane wet forest. The purpose of this study was to investigate the differences between the distribution of terrestrial macroinvertebrate Orders and diversity in primary and secondary forest. It was hypothesized, based on the above information, that primary forest would have greater order diversity but with a lower number of individuals and that secondary forest would contain fewer Orders but more individuals.

MATERIALS AND METHODS

Twenty samples from each forest type were collected from the lower montane wet forest above the Estación Biológica de Monteverde in Monteverde, Costa Rica (Fig 1). Samples were collected in a four-week period from October 20th, 2005 to November 11th, 2005 and within an altitudinal range of 1526 m to 1553 m. Samples were collected randomly by walking the paths of the reserve and visually searching for fallen woody debris. Twenty logs were sampled in primary forest and 20 in secondary forest.

Log dimensions were recorded: length at its longest point, and width at its widest part. Soil temperature beneath the log as also measured.

The penetration test was then performed which involved placing a 1 m long PVC pipe against the top surface of the log and dropping a 22 cm long, 35.71 g screwdriver from the top of the pipe, point down. The pipe was then removed and the amount of screwdriver, in cm, protruding from the log was measured with a ruler. This was done in three places on each log to obtain an average level of rottenness per log. An arbitrary level of rottenness was then assigned based on the average cm of screwdriver protruding: 21.3 to 19 cm of protrusion resulted in a designation of ‘sound,’ logs with values of 18.8

to 18 cm were designated as ‘soft,’ and logs with values of 17.8 to 15.4 cm were designated as ‘very soft.’

Once the penetration test was complete all measurements were complete and the log was flipped over. This was done quickly and away from the collector. A cup was then used to scrape the underside of the log, and to collect all soil directly beneath the log to a depth of 1-2 cm. Soil scoops were emptied into labeled zip-lock bags and taken back to the lab, where they were sorted to remove all macroinvertebrates. Each specimen was preserved in 96% alcohol and identified to the level of Order using a dichotomous key in Borror (1971).

All data were analyzed for diversity with the Shannon-Weiner diversity index during which an evenness and t-test were also performed. Correlation Z tests were also performed on log size (length, width, area) vs. number of Orders and number of individuals, average rottenness vs. number of individuals and number of Orders per log in both primary and secondary forests. A regression was calculated for rottenness versus number of orders per log. T-tests were performed on area of primary forest logs versus area per log of secondary forests, as well as on the average rottenness per log in secondary versus primary forests.

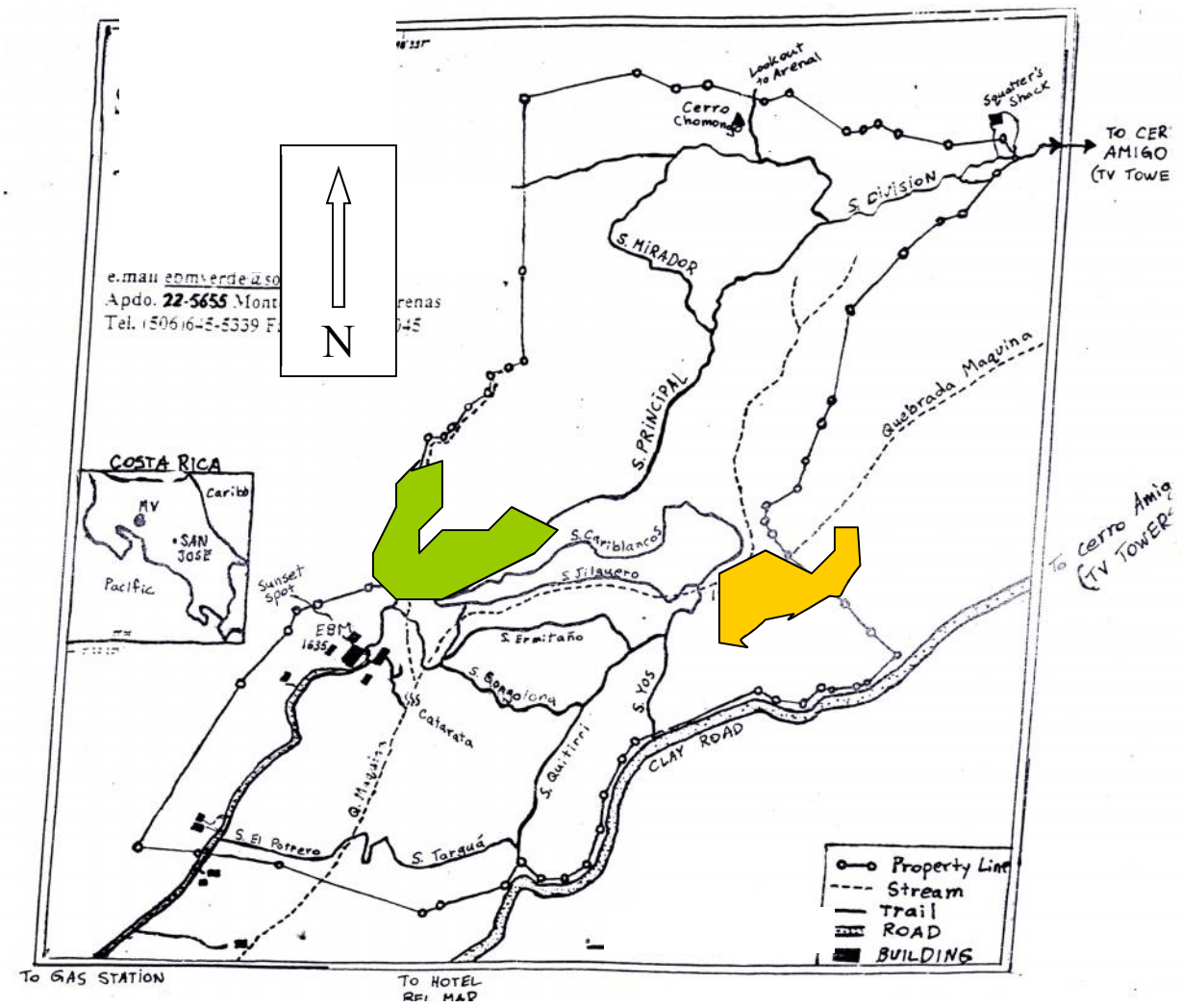

FIGURE 1. Study sites in the lower montane wet forest of Monteverde, Costa Rica where all terrestrial macroinvertebrates were collected. Green site highlighted to the left surrounding 'Bridge' is the location of primary forest collection site. Yellow site to the right near '1545 m' mark is the location of secondary forest collection site. Fall 2005

RESULTS

The log samples demonstrated the following measurements; in primary forest, the average log length was 69.10 cm and the average width was 16.70 cm. The average log area (the average of the product of each logs length and width) was 1159.25 cm^2. The 20 logs average level of rottenness was 18.39 cm, or 'soft'. The average number of individuals collected per log was 5.25 and average orders collected was 1 per log (table 1).

For secondary forest, the average log length was 50.2 cm and the average width was 10.45 cm. The average log area (the average of the product of each logs length and width) was 531.6 cm^2. The 20 logs average level of rottenness was 18.18 cm, or 'soft'. The average number of individuals collected per log was 7.25 and average orders collected was 0.75 per log (table 2).

Primary forest exhibited greater richness (by five Orders), and greater diversity with an H' value of 2.5 as opposed to 2.05 for secondary forest. It also displayed greater evenness (0.84 versus 0.76) primary forest also contained only 105 individuals over 20 logs where secondary contained 145 individuals over 20 logs, which was a significant difference (chi square = 6.4).

TABLE 1. *Primary Forest Average measurements of log length (cm), log width (cm), log area (cm), level of rottenness (cm) as given by a penetration test, number of individuals/log, and number of Orders/log. Averages are of 20 logs measured in primary lower montane wet forest of Monteverde, Costa Rica in Oct and Nov of 2005.*

Characteristic	Average
Average Log Length	69.1 cm
Average Log Width	16.7 cm
Average Log Area	1159.25 cm^2
Average Level of Rot per Log	18.39
Average Number of Individuals per Log	5.25
Average Number of Orders per Log	1

TABLE 2. *Secondary Forest Average measurements of log length (cm), log width (cm), log area (cm), level of rottenness (cm) as given by a penetration test, number of individuals/log, and number of Orders/log. Averages are of 20 logs measured in secondary lower montane wet forest of Monteverde, Costa Rica in Oct and Nov of 2005.*

Characteristic	Average
Average Log Length	50.2 cm
Average Log Width	10.45 cm
Average Log Area	531.6 cm2
Average Level of Rot per Log	18.18
Average Number of Individuals per Log	7.25
Average Number of Orders per Log	0.75

TABLE 3. *Statistical results of a Shannon–Weiner diversity index performed on terrestrial macroinvertebrates in 40 logs. Performed to compare primary and secondary forest diversity, richness, and evenness of Orders in lower montane wet forest of Monteverde, Costa Rica. Each forest type had a sample size of 20 logs, with 40 total logs sampled.*

Index	Primary Forest	Secondary Forest	Significance
S (order richness)	20	15	N/A
H' (Shannon-Weiner)	2.5	2.05	yes t = 3.41
E (eveness)	0.84	0.76	N/A
N (abundance)	105	145	yes chi square = 6.4

Along with the diversity analyses, correlation tests were performed on several of the variables within the data. The only significant correlations were between number of orders per log and log area for secondary forest (table 3, Fig 2), and average rottenness per log versus number of orders and individuals in primary forest (table 4, Fig 3). There was however no significant difference between the levels of rot of logs between primary and secondary forests (t-value = .503, p-value = .6178, df = 38).

A few further findings were on the distribution of Orders between the two forests. Primary forest contained seven Orders unique to primary forest and one unique morpho species. Secondary forest contained one unique Order and one unique morpho species. The two forests had 10 Orders in common, all of which were characterized as generalists by Borror (1971).

TABLE 3. *Secondary Correlation Z test results performed on terrestrial macroinvertebrate order abundance and individual abundance versus log area (cm^2), and average level of rottenness as determined by a penetration test, under which they were found. The sample size of logs was 20. All macroinvertebrates were collected in the lower montane wet forest of Monteverde, Costa Rica in the Estación Biológica de Monteverde reserve.*

Secondary Forest Correlation	Significant	P-value
Log Area vs. Number of Orders	yes	0.0419
Log Area vs. Number of Individuals	no	0.9142
Average Rottenness per Log vs. Number of Orders	no	0.5285
Average Rottenness per Log vs. Number of Individuals	no	0.6434

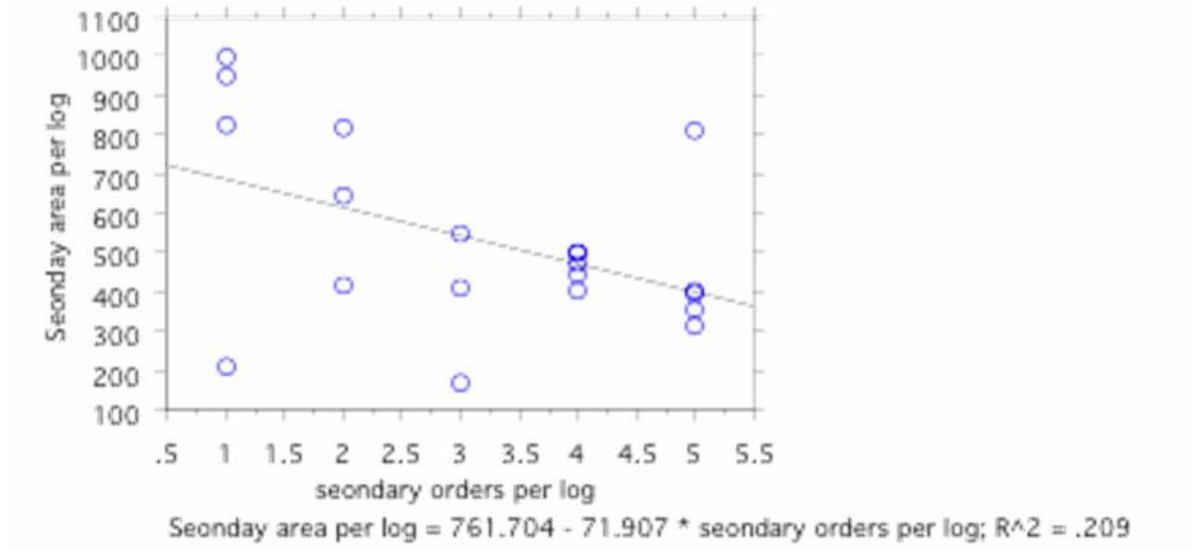

FIGURE 2. Scatter plot and regression line for secondary forest orders per log and area per log in cm^2 . Showing significant correlation between the two variables P = 0.0419. R^2 = .209.

TABLE 4. *Secondary Correlation Z test results performed on terrestrial macroinvertebrate order abundance and individual abundance versus log area (cm^2), and average level of rottenness as determined by a penetration test, under which they were found. The sample size of logs was 20. All macroinvertebrates were collected in the lower montane wet forest of Monteverde, Costa Rica in the Estación Biológica de Monteverde reserve.*

Primary Forest Correlation	Significant	P-value
Log Area vs. Number of Orders	no	0.1288
Log Area vs. Number of Individuals	no	0.5602
Average Rottenness per Log vs. Number of Orders	yes	0.0002
Average Rottenness per Log vs. Number of Individuals	yes	0.0098

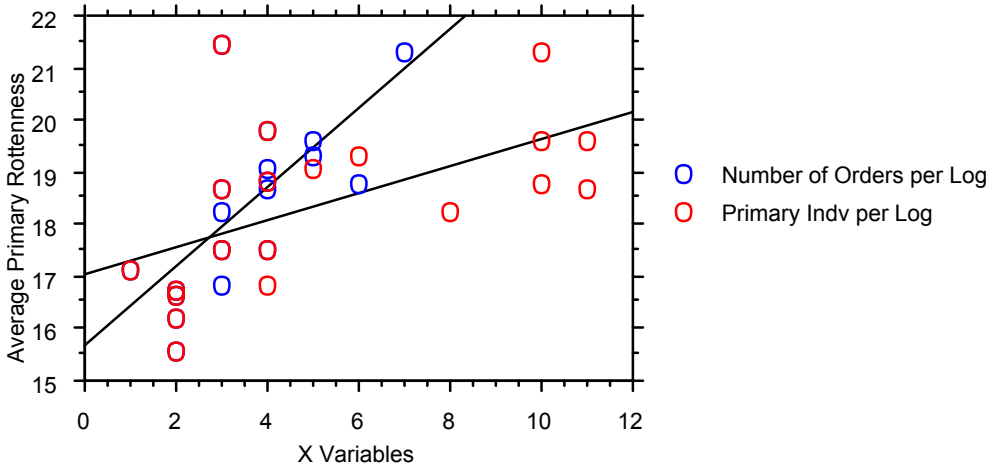

FIGURE 3. Scatter plots and regression lines for primary forest orders per log and individuals per log (X-axis) versus and average rottenness per log. Showing significant correlation between each set of two variables P = 0.0002 for rottenness vs. orders and P = 0.0098 for rottenness vs. individuals.

DISSCUSSION

Based on initial research it was hypothesized that primary forest would contain a greater diversity and lower abundance of macroinvertebrate Orders. Upon review, the data proved to follow the stated hypothesis. The question now becomes, why are there differences observed between secondary and primary forest in macroinvertebrate communities?

Terrestrial macroinvertebrates, just like other tropical taxa, contain both generalist and specialist species (Borror 1964). Also, when deforestation occurs and forest is allowed to regenerate there is a change in plant species composition (Richards 1996). Regenerating tropical forest is characterized by shrubs, climbers and tall herbaceous plants, and as time passes and if the forest is still allowed to regenerate, primary plant species slowly replace secondary species (Richards 1996). This differing spectrum of plant input effects the macroinvertebrate community by inputting different amounts and qualities of organic debris (Wardle et al. 2004).

Certainly a large part of the answer to this question is that terrestrial macroinvertebrates are sensitive to the quality and quantity of organic debris that enter their system (Wardle et al. 2004). A large part of the reason for the differences in macroinvertebrate community would thus be simply that there are differences in organic matter between primary and secondary forest. Although in this study there were no significant difference between the levels of rot in the two forests, the macroinvertebrates of the each still showed differing preferences based on level of rot. Primary forest macroinvertebrates choose logs with a more rotten score on the penetration test. This could be because they are climax community species and are specialized to exploit larger more rotting logs (Borror 1971). There is some factor that goes along with log rottenness that makes these organisms specialize and thus prefer more rotten logs.

As vegetation regenerates in a deforested area there is a large influx of certain vegetative matter (Richards 1996). Thus the macroinvertebrate Orders that are generalists experience a population boom, and more specialized Orders decline or vanish locally. This would explain there being less Orders present in secondary forest, but more individuals representing those fewer Orders. Those Orders that are present represent more generalist Orders, or predators there of. As time goes on, as more plant species invade, the diversity will increase as specialists arrive to capitalize on the new climax plant species emerging, and abundance will decrease since the given amount of any one resource would decrease with greater diversity.

Studies done in New Zealand found that with changes in flora communities the major soil inhabitant composition changed, yet a few groups did not change with the change in flora (Wardle et al. 2004). Similarly, this study's findings for Costa Rican macroinvertebrates; found that although there were differences in diversity, there were several Orders in common between the two forest types that exhibited similar abundances.

To address the finding of secondary fauna significantly choosing smaller logs more often, this is likely caused by it simply being the more abundant resource present the average area per log between secondary and primary forest was statistically significant (Chi square = 245.46 with 1 degree of freedom.) So the generalists were just doing what they do best, monopolizing the most abundant resource that they can.

These results speak closely to the current environmental conditions of the world, and especially the tropics. Much of the forested world now consists of secondary forest and every bit of knowledge on the regeneration of such areas is valuable, perhaps working from the bottom up would be a new effective restoration management technique. It would likely prove further insightful to conduct this study to the level of species and subsequently examine the natural history of the species in correlation with their collection site. It would also prove insightful to study terrestrial macroinvertebrates not confined to areas under logs, but to compare communities between different plant communities. These studies, along with studies similar to this one could likely be used as kinds of bio-indicators to assess the speed and level of recovery of regenerating habitats around the world.

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Appendix

TABLE 4. *Catalogue of macroinvertebrate Orders found in the secondary forest of lower montane wet forest in Monteverde, Costa Rica. Sample size was 20 logs. Collected in Oct and Nov of 2005.*

Macroinvertebrate Order	Individuals Found
Acari	4
Amphipoda	6
Araneae	14
Coleoptera	14
Glomerida	2
Hemiptera	2
Homoptera	1
Hymenoptera	2
Isopoda	54
Isoptera	1
Maggot	9
Orthoptera	12
Polydesmida	21
Scolopendromorpha	2
Scutimorpha	1
Total # of macroinvertebrates collected	145

TABLE 5. *Catalogue of macroinvertebrate Orders found in the primary forest of lower montane wet forest in Monteverde, Costa Rica. Sample size was 20 logs. Collected in Oct and Nov of 2005.*

Macroinvertebrate Order	Number Found Total
Acari	6
Amphipoda	8
Araneae	5
Coleoptera	11
Dermaptera	2
Diplura	1
Geophilomorpha	1
Glomerida	2
Hemiptera	5
Hymenoptera	5
Isopoda	28
Isoptera	2
Orthoptera	14
Polydesmida	4
Polyxenida	2
Pupae	1
Scolopendromorpha	3
Scutigeromorpha	1
Snail	1
Spirobolida	3
Total # of Macroinvertebrates Sampled	105