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Diversity and Composition of Insects in a Regenerated Premontane Tropical Forest

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ABSTRACT

Tropical forests, the richest ecosystems on earth, are rapidly disappearing. This is causing the loss of species at an unprecedented rate. However, there is hope to regain lost biodiversity through the process of forest regeneration. Insects, the most speciose class of animals, are concentrated in the tropics. I examined the effects of reforestation on insect species composition and diversity in the canopy and understory of a premontane tropical forest in Monteverde, Costa Rica: La Calandria. I collected insects with flight interception traps and analyzed the composition and diversity of orders and hymenopteran morphospecies. I found that species composition varies with reforestation status and between the forest canopy and understory. Although the species composition is different, I found diversity between less disturbed and regenerated forest to be similar.

Diversidad y composición de insectos en un bosque tropical premontano

RESUMEN

Los bosques tropicales son los ecosistemas más ricos de la tierra, pero están desapareciendo rápidamente. Esto está causando una pérdida de especies a un ritmo sin precedentes. Sin embargo, hay esperanza de recuperar la biodiversidad perdida a través del proceso de regeneración de los bosques. Los insectos, la clase más especiosa de animales, se concentran en los trópicos. Examiné los efectos de la reforestación en la composición y diversidad de las especies de insectos en el dosel y el sotobosque de un bosque tropical premontano en Monteverde, Costa Rica: La Calandria. Recolecté insectos con trampas de intercepción de vuelo y analicé la composición y diversidad de órdenes y de morfospecies de himenópteros. Descubrí que la composición de las especies varía según el estado de reforestación y entre el dosel del bosque y el sotobosque. Aunque la composición de las especies es diferente, encontré que la diversidad entre bosques poco perturbados y regenerados es similar.

Tropical forests are the most speciose ecosystems on earth, supporting more than half of all extant species (Gentry, 1992). Most “biodiversity hotspots” are located in tropical forests (Myers et al., 2000). Hotspots are ecosystems with particularly high concentrations of endemic species undergoing rapid habitat loss (Myers et al., 2000). Arthropods, specifically insects, are concentrated in tropical forests (Wilson, 1989). Although close to 900,000 species of insects have been described, the total number of insect species is estimated to be around 10,000,000 (Gaston, 1991).

As the “last biological frontier,” the forest canopy is a relatively untapped source of tropical biodiversity. Specifically, arthropods in the canopy remain widely understudied (Erwin, 1983). Many undescribed insect species are suspected to exist in the canopies of tropical forests (Erwin, 1983). Additionally, the species composition of the forest canopy is often strikingly different from the understory (Longino & Nadkarni, 1990).

However, despite the richness of tropical forests, we are currently in the midst of a “biodiversity crisis” (Wilson, 1989). Species are disappearing far faster than we are able to describe them. Because the planet’s insect species are largely undescribed and unstudied, biodiversity loss is a threat with unpredictable consequences (Wilson, 1989). Deforestation is a major cause of the rapid loss of species in the tropics (Wilson, 1989). Agricultural production is one of the most significant causes of deforestation, as growing urban populations require increasing amounts of food produced in rural tropical areas (DeFries et al., 2010). Population growth is projected to occur in mostly urban areas, which counterintuitively has a larger impact on tropical deforestation than rural growth (DeFries et al., 2010). Urban populations consume more processed food and animal products than their rural counterparts, placing more agricultural pressure on tropical forests (DeFries et al., 2010).

In response to biodiversity loss, reforestation and reclamation of agricultural sites is becoming more common. DellaSala et al., (2003) define the core principle of forest restoration, ecological integrity, as “the ability of an ecosystem to support and maintain a balanced, adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of natural habitats within a region.” Insect community structure is an overall indicator of forest biodiversity, ecosystem integrity, and the recovery of ecosystems following human disturbance (Maleque et al., 2006). However, reforested areas are often novel in terms of species composition, species interactions, and ecosystem functions (Aerts & Honnay, 2001).

I investigated insect composition and diversity in an undisturbed secondary forest as well as two reforested plots in a premontane forest in Monteverde, Costa Rica. I examined the effects of reforestation on the understory and canopy of a plot that was reforested by tree planting and a former agricultural plot allowed to regenerate naturally. The central question addressed by this study is as follows: how does reforestation affect insect composition and diversity in the tropical forest understory and canopy?

MATERIALS AND METHODS

Study Site

This study took place at La Calandria Reserve in Los Llanos, Costa Rica, from 13-18 May, 2019. La Calandria is mid-elevation (1200-1250m) and is on the border between premontane moist and premontane wet forest. I collected insect samples from three plots: one undisturbed secondary forest (>50 years old) and two reforested plots. One plot was reforested by planting in 2001. The other plot is a former coffee plantation that has been re-colonized by natural revegetation, beginning in the 1990s.

Insect Trapping

I collected flying insects with simple flight-interception traps based on those used by Barbier, 2019 and Steininger et al, 2015. These traps consist of two-liter soda bottles with window cutouts, filled with water, unscented soap and ethanol and suspended from tree branches with nylon (Figure 1). I colored the traps yellow to attract Hymenoptera, my focal order. Disposable plastic plates were placed over the top to prevent flooding from rainfall (Figure 1). I installed four traps in the understory of each plot, suspended 0.5m from the ground. Two traps were placed in the canopy of each plot. Traps were active for approximately five days, wherein they were checked and emptied twice.



Figure 1. Flight interception trap model. Insects entered through the window and made contact with the smooth plastic interior, causing them to fall into the water.

Insect Sorting

I combined trap samples from each plot into the categories “Planted,” the plot reforested by tree planting, “Abandoned,” the abandoned coffee plantation reforested by natural regeneration, and “>50,” or the plot of undisturbed secondary forest. From there, samples were split into canopy and understory specimens. Within each of the six categories, I identified specimens to order and recorded the number of individuals and morphospecies. Furthermore, I selected all hymenopterans from each category and recorded which morphospecies were present.

Analysis

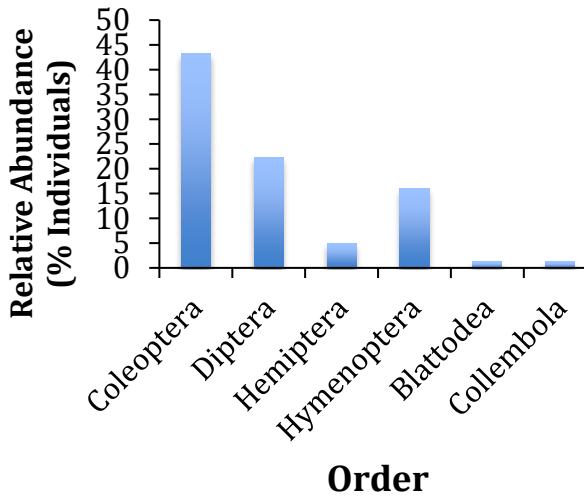
I analyzed the composition of the understory and canopy of each plot on two taxonomic levels, arthropod orders and morphospecies of Hymenoptera. I compared the abundance of each order within each of the six categories and identified which were dominant, or most abundant.

To assess diversity, I used a true diversity test with three levels of analysis. $q=0$ is a equal to richness, $q=1$ (Shannon index exponent) weighs common species more heavily, and $q=2$ gives more weight to rare species. True diversity indices were calculated for the canopy and understory of each plot with regards to order richness (number of morphospecies/order) and hymenoptera morphospecies richness. I also compared the number of morphospecies of each order within the understory and canopy of each plot.

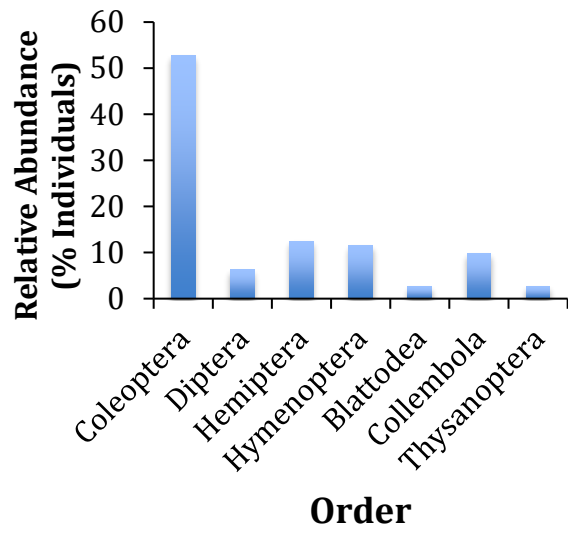
Order Composition

I collected 521 total individuals over the course of five days. Relative abundance of arthropod orders varied between plots and within plots between canopy and understory (Figure 2). In the understory of all three plots, the significantly dominant order (by abundance of individuals) was Coleoptera, followed by Diptera and Hymenoptera respectively. However, in the canopy, Coleoptera was only dominant in the planted plot. In the >50 year undisturbed plot, Hymenoptera dominated, followed by Coleoptera and Diptera. In the abandoned pasture, Diptera and Hymenoptera were the most dominant, followed by Coleoptera.

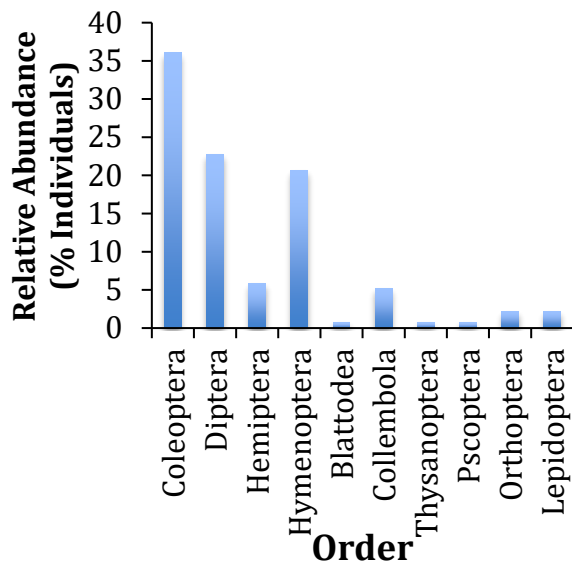
A



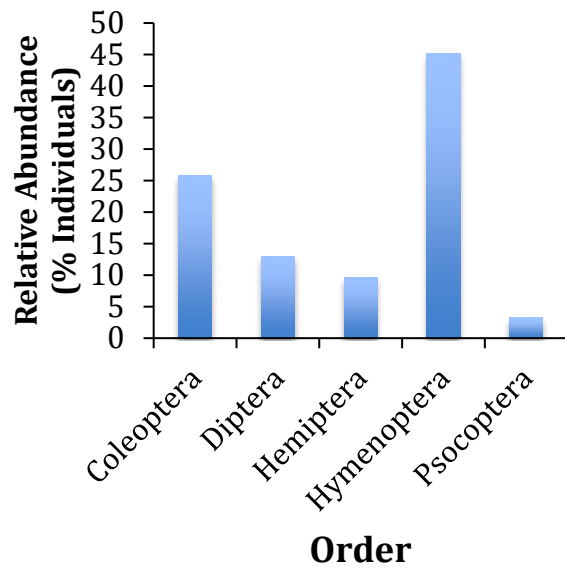
B



D



C



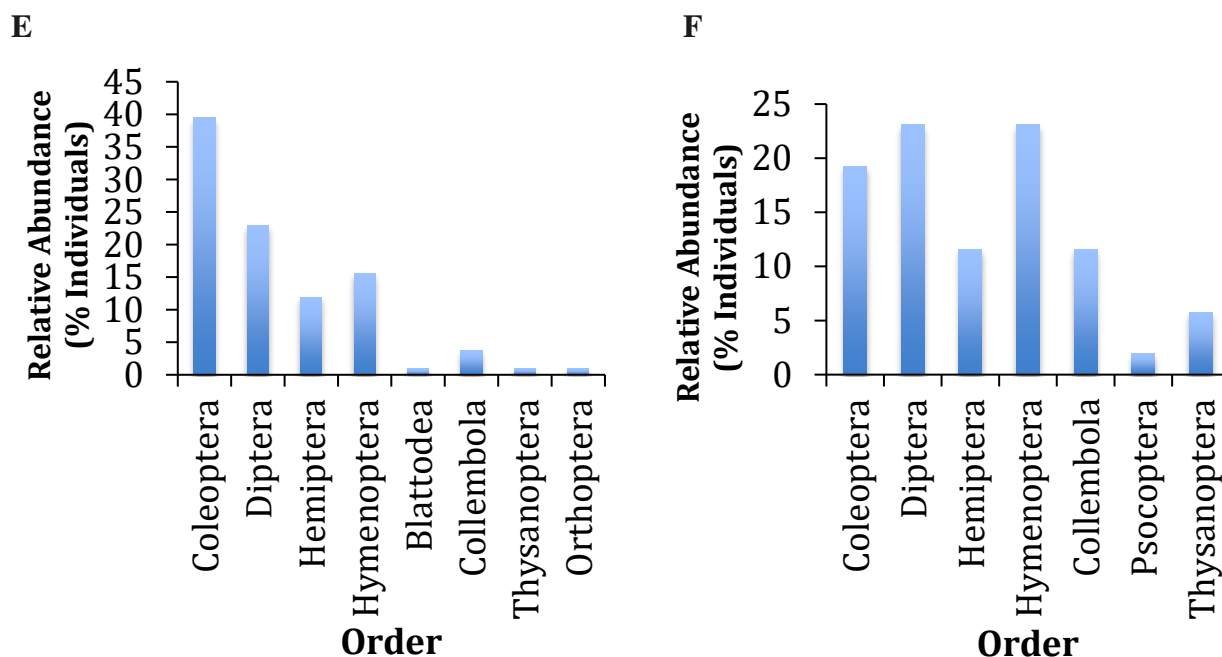


Figure 2. Order composition of each plot, separated into understory and canopy. Measured by relative abundance of each order. (A) Planted, Understory (B) Planted, Canopy (C) >50, Understory (D) >50, Canopy (E) Abandoned, Understory (F) Abandoned, Canopy.

Table 1. Chi Square values of order abundances. Numbers of individuals from each order were compared within each of the six categories.

	Understory	Canopy
Planted	95.691, p<0.01	176.429, p<0.01
>50	201.026, p<0.01	24.548, p<0.01
Abandoned	135.985, p<0.01	20.923, p<0.01

Morphospecies Composition

When comparing Hymenoptera between all six categories, I identified 54 distinct morphospecies. I compared the morphospecies found in the understory and the canopy of each plot (Figure 2). The abandoned pasture had significantly more morphospecies in common between the canopy and understory than did the planted plot or the undisturbed forest ($X^2=7.0$, $p<0.05$).

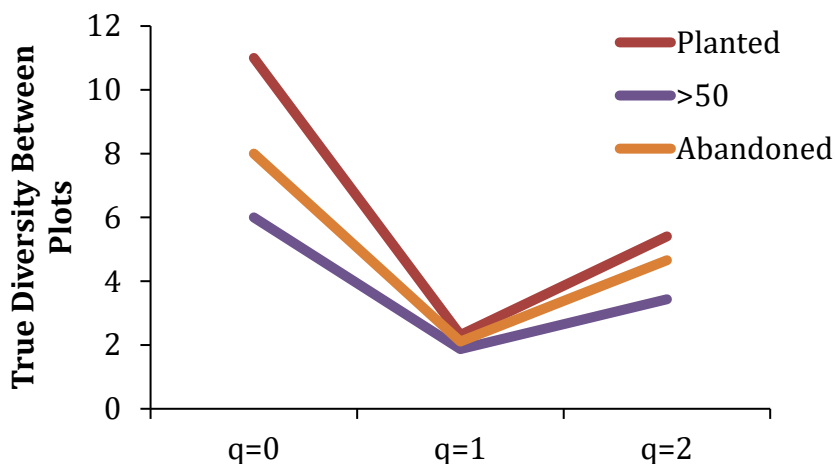
Table 2. Hymenoptera morphospecies comparison between canopy and understory of each plot. Abandoned plot has significantly more species in common between canopy and understory.

	Present in Canopy	Present in Understory	Present in Canopy and Understory	Total
Planted	7	11	0	18
>50	13	13	1	26
Abandoned	17	13	5	25

Order Diversity

True diversity indices showed no significant difference between the order diversity (morphospecies/order) of each plot in both the canopy and understory (Figure 3). Order richness ($q=0$) did not vary significantly between any plot (Understory $X^2=0.05$, $p > 0.70$, Canopy $X^2=1.52$, $p > 0.40$). However, when comparing the number of morphospecies within each order, certain orders were significantly diverse in some plots. Coleoptera was significantly more diverse in the understory of both the abandoned plantation and the >50 year forest ($X^2=6.14$, $p < 0.05$). In addition, Coleoptera and Hemiptera were significantly more diverse in the canopy of the planted plot (Coleoptera $X^2=30.46$, $p < 0.01$, Hemiptera $X^2=7.53$, $p < 0.05$).

A



B

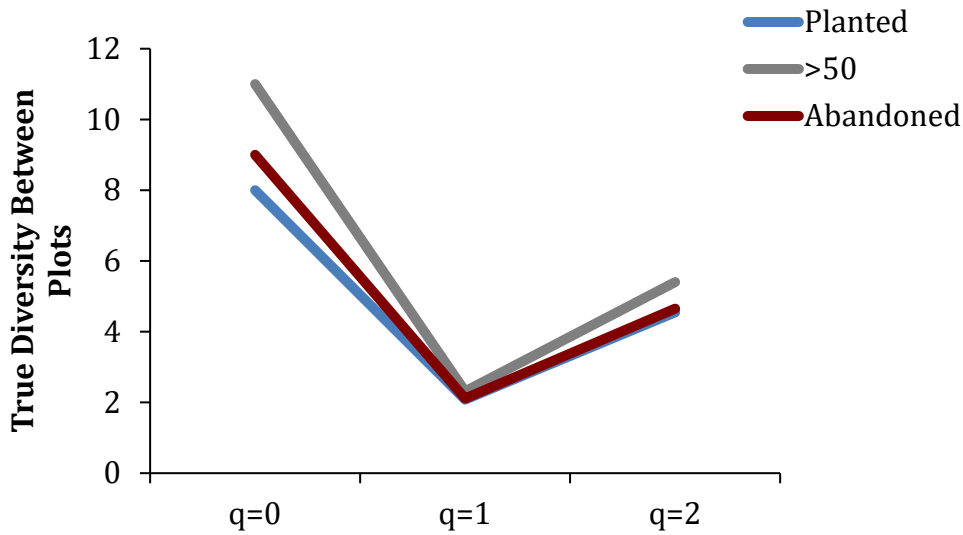
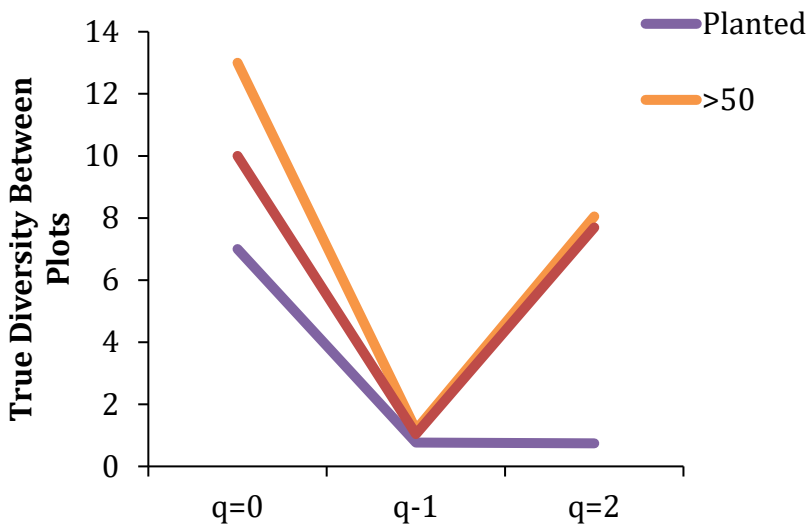


Figure 3. Order true diversity index results for A) Canopy and B) Understory for each plot. Diversity is not significantly different between plots.

Hymenoptera Morphospecies Diversity

Hymenoptera morphospecies diversity did not significantly differ between any of the plots, with the exception of diversity with weight given to rare species ($q=3$) in the forest canopy (Figure 4). The undisturbed plot was significantly lower than the other two ($X^2=6.18, p<0.05$).

A



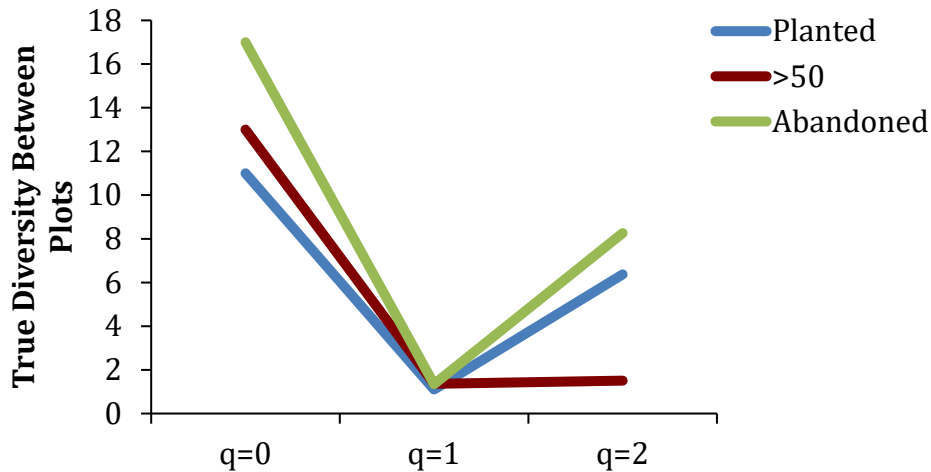
B

Figure 4. Hymenoptera morphospecies true diversity index results, compared between plots. A) Canopy and B) Understory.

DISCUSSION

Order composition varied between each category. Certain orders, such as Lepidoptera, were found in only one category. Most noticeable is the variation in the canopy, where the dominant order differed between each plot. While Coleoptera, Hymenoptera, and Diptera were most abundant, this is likely due to the mechanism of the traps. These traps did not include bait and were designed to capture flying insects. For a more complete picture of order composition, traps directed towards walking insects would also be needed. Regardless of the most abundant orders, these data demonstrate that differences in composition exist between the canopy and the understory. Furthermore, this result supports the idea that regenerated forest can be novel in taxonomic composition (Aerts & Honnay, 2001). Changes in species composition result in changes to ecological interactions, potentially preventing forests from returning to their previous ecological function.

Hymenopteran morphospecies composition also varied between plots and between the canopy and the understory. Relatively few species were shared between the canopy and understory of the planted and undisturbed forests, while the abandoned pasture had significantly more in common between the two layers. This could imply that the abandoned pasture supports more habitat generalists than the other plots.

While species composition varied between plots, each plot was largely equal in diversity in both arthropod orders and hymenopteran morphospecies. This result bodes positively for restoration efforts, implying that reforested plots can hold similar levels of biodiversity as undisturbed plots. When Maeto et al. (2006) examined the effect of forest regeneration on braconid wasps in tropical Asia, they too found varying species composition yet similar levels of diversity between undisturbed and reforested plots. A notable exception to the general trend is the undisturbed secondary forest understory, which had significantly fewer rare species than the reforested plots. There is more than one explanation for this result. As the vegetation regenerates

and arthropod species colonize new land, it may take time for once-abundant species to regain former population levels. Contrastingly, novel plant species composition in reforested plots could present a different set of resources for arthropods to exploit, causing species that were once common in these forests to become rare.

Diversity within order varied between plots as well as canopy and understory. While Coleoptera was significantly less diverse in the understory of the planted plot, the same order was significantly more diverse in the canopy. Hemiptera was also significantly more diverse in the canopy of the planted plot. As hemipterans are largely herbivorous, this could indicate higher plant diversity in the canopy of this plot. Alternatively, fast-growing plants are often planted during reforestation (Wightman et al., 2001). These trees produce less secondary metabolites than slow-growing species, and are thus subject to increased levels of herbivores (Coley et al., 1985). Increased diversity of hemipterans may be in response to the tree species chosen for planting in this plot.

Overall, this study holds important implications for forest restoration ecology. It is important to consider that the forest understory and canopy are different with respect to species composition and diversity within arthropod orders. When measuring and describing forest biodiversity, it is imperative to treat each layer as a separate ecosystem. Furthermore, these results indicate that arthropod diversity can be recovered in a relatively short amount of time. Overall, forest restoration is an imperfect, but viable solution to insect biodiversity loss.

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