Research

Above and below ground impacts of terrestrial mammals and birds in a tropical forest

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Understanding the impact of losing trophic diversity has global significance for managing ecosystems as well as important theoretical implications for community and ecosystem ecology. In several tropical forest ecosystems, habitat fragmentation has resulted in declines and local extinctions of mammalian and avian terrestrial insectivores. To assess the ability of a tropical rainforest community in Ivory Coast to resist perturbation from such loss of trophic diversity, I traced feedbacks in above and below ground communities and measured changes in nutrient levels and herbivory rates in response to an experimental exclosure of avian and mammalian terrestrial insectivores. I present evidence that loss of this functional group may result in increased tree seedling herbivory and altered nutrient regimes through changes in the abundance and guild structure of invertebrates. Exclusion of top predators of the forest floor resulted in increased seedling herbivory rates and macro-invertebrate (>5 mm) densities with strongest effects on herbivorous taxa, spiders and earthworms. Densities of microbivores including Collembola, Acarina and Sciaridae showed the opposite trend as did levels of inorganic phosphorus in the soil. Results were evaluated using path analysis which supported the presence of a top down trophic cascade in the detrital web which ultimately affected turnover of phosphorus, a limiting nutrient in tropical soils. Results illustrate the potential importance of vertebrate predators in both above and belowground food webs despite the biotic diversity and structural heterogeneity of the rainforest floor.

Understanding how trophic interactions among species in a food web affect ecosystem processes has become a central challenge in ecology and conservation biology in the last decade. This surge of interest has arisen in part because of an increasing concern for the global decline of biodiversity and recognition of the importance of maintaining functioning ecosystems (Chapin et al. 2000, Hoekstra et al. 2005). For aquatic systems, numerous studies have shown how changes in densities of a top predator can lead to cascading changes in communities and ecosystem processes through effects on consumers (Strong 1992, Schmitz et al. 1997, Duffy 2002). In the more complex terrestrial systems, a single species may have less impact on its community and indirect effects of intense trophic interactions within the food web tend to dampen more strongly than in aquatic systems leading to more of a "trickle" than a "trophic cascade" (Halaj and Wise 2001, Shurin et al. 2006).

Cascades of species interactions in terrestrial systems may be quite important for managing natural terrestrial systems however, when certain functional groups of species tend to be particularly sensitive to anthropogenic or other disturbances (Turner 1992). Therefore, one priority for further development of terrestrial ecology is to understand impacts of losing functional or trophic diversity from food webs on ecosystem processes. Losing trophic diversity may have strong effects on ecosystem processes (Raffaelli 2004)

through direct interaction with the environment or through second-order or higher effects (Turner 1992).

An example of trophic diversity loss occurs in disturbed tropical rain forests where evidence suggests that understory insectivorous birds (Sekercioglu 2002, Sodhi et al. 2004, Gray et al. 2007) and sometimes mammals (Goodman and Rakotondravony 2000, Martin 2003) tend to be sensitive as a group to forest fragmentation and degradation. This trophic group preys upon consumers of both above and belowground food webs and thus has a strong potential for indirectly altering ecosystem processes such as herb layer herbivory and nutrient turnover in rain forest (Sekercioglu 2006). Alternatively, complex terrestrial systems such as rainforests may resist such perturbations because the high biotic diversity and functional redundancy of both predators and prey may buffer or compensate the effects of species loss (Strong 1992).

The ability of mammals and birds to affect ecosystem function through trophic interactions in the detrital web is especially contentious. There is a general view that the low biomass and sporadic occurrence of vertebrates in the forest offers little potential to regulate organisms near the base of the food web living in a structurally complex environment (Setälä et al. 1998, but see Wyman 1998, Walton 2004). Empirical work that has focused on predation in detrital systems, has generally focused on the roles of predaceous

mites, nematodes, and, more recently, spiders (Lawrence and Wise 2000, Moran and Alison 2002, Miyashita and Niwa 2006). Ecosystem influences of higher trophic levels, however, are often disproportionate to their biomass (Turner 1992) and roles of vertebrate predators should be considered if we are to understand their potential effects on ecosystem processes.

To assess how the above and below ground communities and ecosystem processes of a rainforest understory respond to or resist effects of altered trophic diversity, I mounted a 10 month exclosure experiment in the rainforest of Ivory Coast. I traced feedbacks in above and below-ground communities and measured changes in nutrient levels and herbivory rates in response to an experimental exclosure of avian and mammalian terrestrial insectivores. Specifically, the experiment addresses two main questions. First, does the complexity of the rainforest system enable it to resist perturbations in trophic diversity of top predators such that communities and ecological processes are not affected? And, secondly if effects do occur above ground, do characteristics of below ground food webs such as higher physical and biotic heterogeneity, provide a buffer to resist effects of such perturbation?

Methods

Research site

I tested the effects of the terrestrial insectivorous guild of mammals and birds on the understory community using exclosure experiments in the lowland, evergreen rainforest (elevation 80–623 m) of Taï National Park, Ivory Coast. Experiments were conducted from 12 March 2001 to 20 December 2001, near the Station de Recherche en Ecologie Tropical (5°50′003″N, 007°20′536″W). Taï National Park comprises 450 000 ha and is the largest protected lowland forest in west Africa (Poorter et al. 1994).

The main terrestrial avian insectivores observed in this forest were the large-bodied terrestrial Galliforme birds including Latham's francolins, *Francolinus lathami*, white-breasted guinea fowl, *Agelastes meleagrides,* and buff-spotted flufftails, *Saruthrura elegans*. Though relatively common around the study site, these birds are mostly absent in forest remnants because of their strict habitat requirements and limited dispersal abilities (Gatter 1997). The major mammalian insectivores in the forest understory included the mongooses (western cusimanse, *Crossarchus obscurus,* and Liberian mongoose, *Liberiictis khuni*) and white-toothed shrews, *Crocidura* sp. Most species of white-toothed shrews of west Africa live at low densities and they are listed as threatened by IUCN because of habitat loss and fragmentation (IUCN 2007). Mongooses have the potential for considerable impact on the invertebrate fauna because of their quick metabolisms (relative to mammals of similar size) and high densities in the forest (Waser 1980). Yet, as in other areas in Africa (Maina and Jackson 2003), forest specialist mongooses may be absent or declining in secondary forest and forest fragments due to human hunting and habitat specificity (Taylor 1992, Caspary 1999).

Experiments

Seven plots were used for this experiment; each consisted of two, 9 m^2 (3 × 3 m) subplots (control and exclosure) separated by a 3 m buffer zone to avoid possible edge effects of exclosure fencing. A two-month pilot study carried out the year prior to this one suggested that seven plots would be sufficient for detecting significant differences among treatments. Plots were spaced approximately 200 m apart and treatment was assigned randomly to one of each pair of subplots. Each exclosure subplot was fenced with nylon mesh (opening, 25 mm^2) to exclude terrestrial, insectivorous mammals and birds. The mesh openings exceeded the width of most invertebrates present and allowed unhindered movement to all but the very large species. The base of the fencing was buried 20 cm below the ground, and walls were 80 cm high. Ground litter and branches were disturbed as little as possible while installing the fencing. All fallen branches were left intact within the fenced plots by sawing the ends where the fencing was to be placed. This was to avoid the effects of disturbance and habitat change on both the invertebrates and seedlings. The tops were left open to allow invertebrate dispersal, litter accumulation, and to minimize differences in microclimatic conditions. While this permitted smaller arboreal birds to enter, the large-bodied terrestrial Galliformes, suspected to be most prone to extinction in fragmented areas, were excluded. Biweekly census of fenced areas for animal signs revealed no evidence of intrusion by terrestrial mammals or Galliforme birds. In contrast, signs of insectivorous mammals and birds on control plots were frequent (≈1 visit per 10 days) and included footprints and ground scrapes.

Baseline estimates of macro and micro-invertebrate abundances were collected from 12 to 15 March 2001 and fences were subsequently erected around exclosure subplots. None of the invertebrate groups identified during the pre-treatment census differed significantly in abundance between control and exclosure subplots (paired t-tests, p > 0.40 for each taxon). Control subplots were marked with inconspicuously colored nylon string. Subplots were monitored for macro-invertebrate (longer than 5 mm) abundance at ≈4-week intervals (mean =26.6 days) for the duration of the experimental period (except May). Each census period required three to five consecutive days to complete. During census periods, invertebrates were sampled between 11:00 and 13:00 using a non-destructive visual sampling. Macro-invertebrate counts were done within three 50 × 50 cm quadrats chosen randomly at each census period from an imaginary grid of quadrats (6 × 6 quadrats) within each subplot. Invertebrates were identified alive and returned into litter adjacent to the plots (Moya-Larano and Wise 2007). A single observer sampled quadrats by searching the vegetation, leaf litter, and surface roots and counting all macro-invertebrates encountered during five minutes of search time. All invertebrates were identified to order. To reduce disturbance to the populations, only unrecognized specimens were collected for identification. This method was used as a relative index of arthropod abundance because it roughly mimics the process insectivores use during foraging.

Termites and driver ants (*Dorylus* sp.) are commonly seen in massive swarms on the forest floor; however, their

patchy distribution and high mobility did not allow for accurate counts nor were their populations likely affected by the patchy exclosure treatments. Because of this, such manipulation is also likely to have a negligible effect on the rates of predation by driver ants. Therefore, only individually foraging ants and termites were included in the analysis. Since driver ants (like neotropical army ants) are also known to be sensitive to forest fragmentation and extremely important predators of invertebrates, results of this experiment may be conservative with respect to fragmentation effects on invertebrate communities.

Sticky traps were used to sample micro-invertebrates (< 5 mm) of the forest floor. While these traps are typically used to sample flying insects, sticky traps also provide an excellent method for evaluating microinvertebrates of the leaf litter such as collembolan and mite populations. These micro-invertebrates can initially walk across the surface of the traps but eventually sink and become stuck in the medium. This allows for a higher sampling rate than other methods such as pitfalls (Dunham unpubl.) and requires much less effort, time, and materials than the standard Burlese funnel method. The sticky traps were made by mounting insect grade tangle-foot tape on a cylinder that was 5 cm diameter and 10 cm length. Sticky traps were stabilized on the ground in an upright position with a wooden stake placed through the center of each cylinder. I placed one trap in the center of each exclosure and control subplot. After seven days, the traps were removed and cut open to lay flat for analysis. All arthropods were counted and identified to order in the lab using a dissecting scope. Because sticky-trap sampling is destructive to the population, it was done only at the end of the experiment to avoid altering abundances throughout the experiment. Two of the seven plots were discarded from the analysis because the traps became covered in debris after a heavy rain. Results should be thus interpreted with these limitations in mind.

Earthworm densities were sampled on the same day that sticky traps were collected and only once since sampling earthworms requires high levels of soil disturbance. Three $25 \times 25 \times 10$ cm soil samples were collected from each treatment plot and the wash and sieve method was used to extract worms.

Herbivory

Herbivory of seedlings was measured within the subplots to examine the effects of vertebrate exclosure. In May 2001, 20 seedlings in each subplot were chosen by selecting those 20 closest to the center point of each subplot. Each seedling was marked by tying color coded nylon string around the first internode below the apical bud. I marked unexposed leaves to avoid biased sampling and to ensure leaves were of the same maturity. After four weeks, emergent leaves were monitored for damage by insect herbivores. Insect herbivory could be easily distinguished from duiker, *Cephalophus* sp., and other mammalian herbivory because mammalian herbivores girdle or clip seedlings at the stem. Within the control sites, 6.1% of leaves monitored were affected by duiker herbivory. Each leaf was characterized visually according to herbivory intensity (proportion eaten). Leaf herbivory, expressed as a proportion of the leaf missing, has

advantages over leaf area measures because, unlike absolute area lost, the proportion missing, does not change as areas consumed in a young leaf expand as the leaf grows (see Reichle et al. 1973 for more details on this method). An analysis showed no significant difference in morpho-species composition between paired subplots. Mortality of seedlings due to invertebrate herbivory was also recorded after two months of observation.

Litter consumption

I examined whether litter consumption and fragmentation by invertebrates on the forest floor was affected after eight months of vertebrate exclusion. The tagged leaf method was used instead of using the traditional litterbag method. Litterbags tend to measure the effect of soil fauna on litter fragmentation rates compounded by the effect of microbes. For this reason, I used percent of dead-leaf area lost to invertebrates as a measure of the effects of litter fragmentation rates in exclosure and control treatments. This method directly measures the effects of the invertebrates that mechanically fragment and ingest litter in a way similar to the herbivory measurements taken in this study. These include mainly the macro-invertebrates including termites, millipedes, and isopods. Five senesced leaf samples were cut (5×5 cm) from freshly fallen (>1 day) leaf litter collected from the same tree (*Entandophragma*) with plastic sheeting placed under the canopy. Litter squares were placed in the center of each subplot, equally spaced in a ring formation (20 cm diameter). After 20 days of exposure, remaining fragments were collected and they were pressed and dried for later analysis. The senesced leaf area loss was measured with a 1×1 mm grid and comparisons were made between control and exclosure treatments.

Nutrient cycling

In situ soil-incubation experiments were conducted to determine if insectivores affect N and P content of the soil. The incubations were placed in the center of each of the fourteen subplots. Soil was isolated from the surrounding soil with a circular metal blade (8 cm diameter and 20 cm depth) and cleared of aboveground vegetation. The edge of the soil column was lined with plastic sheeting to prevent roots from re-entering. This was done to prevent active uptake of these nutrients by plants and their associated mycorrhizae. This uptake is particularly efficient in tropical rainforests and can minimize differences found between samples. Incubations were covered with a plastic lid which was elevated approximately 1.5 cm to inhibit water and nutrient runoff but to allow invertebrate access. The incubation period lasted 20 days, and began between 18 and 19 November 2001. At the end of 20 days of incubation, the soil was removed for analysis. Soil samples were immediately sifted (2×2 mm sift) to remove debris and oven dried at 70°C (until mass remained constant) to avoid microbial conversion of N and P. Samples were then stored in an airtight container for later analysis.

All soil samples were analyzed at Kansas State Univ. Soil Testing Laboratory. Ammonium and nitrate were extracted with 1 M KCl from 2 g of soil. A cadmium reduction was

applied to the extracted nitrate. Levels of both were determined through colorimetric assays run in separate channels in a flow analyzer to measure the ions simultaneously. Ammonium and nitrate were summed as extractable N. Inorganic P was extracted with the Bray P-1 technique. This method uses an HCl-ammonium fluoride extractant and a colorimetric assay to determine inorganic (plant available) P.

Data analysis

I used a general linear mixed model ANOVA with repeated meastures (PROC MIXED, SAS Inc.) to test for the effects of predator exclosure and month of census on overall invertebrate densities. Exclosure treatment was used as the fixed effect; plot was treated as a random effect, and month as repeated factor to account for the covariance of repeated observations within replicates. Block effects were tested using a one-tailed log-likelihood ratio χ^2-test (Littell et al. 1996). Exclosure effects on individual taxa were measured using a split-plot ANOVA with exclosure as the main effect; a sequential Bonferroni adjustment was applied to the multiple tests to limit type I error. For all analyses, log transformations were done when necessary to achieve normality of data.

Because of all the possible indirect effects occurring as a result of exclosure studies, mechanistic interpretation of results is difficult. However path analysis can be used to examine cause-effect hypotheses, which is logistically more feasible than exhaustive pair-wise experimental analysis and provides a stronger inference than simply employing regression techniques (Wootton 1994). Based on the results of the experiment, I used path analyses to evaluate hypotheses about how predator exclusion might have altered nutrient levels and microbivore densities. I used this method to distinguish between possible bottom up effects caused by changes in nutrient addition (exclusion of vertebrate excretion) or top down interaction effects which may have occurred through trophic and/or indirect behaviorally mediated effects of predator exclusion. To determine whether top-down or bottom-up forces are more likely to be driving the effects, I compared path analyses results and chose the best fitting model. Path analyses were done with AMOS 7.0 software (Arbuckle 2006).

Results

Invertebrate densities

Macro-invertebrates in control and exclosure subplots showed correlated temporal trends in numbers, likely due to abiotic conditions such as rainfall and resource availability (Fig. 1a). In October, flooding of the forest floor occurred during torrential rains, which may have resulted in the population decline observed for both treatments. The seasonal effect on macro-invertebrate densities was significant (effect of month: $F_{6,36} = 4.36$, p = 0.002). Despite strong seasonal effects, exclusion of vertebrate predation resulted in significantly higher macro-invertebrate densities ($F_{1,6} = 14.44$, p = 0.009). Interaction effects between season and exclosure treatment were not significant ($F_{6,36} =$

1.12, p = 0.371). The abundance of macro-invertebrates in exclosure subplots ranged between 47% and 102% (mean = 55.6 ± 18%) higher than in control subplots during the experiment.

Orthoptera, Blattaria, Isopoda, Araneae, Hymenoptera, Isoptera and Myriapoda made up 94.7% of all macro-invertebrate counts. Rare taxa (>6% of total) included Coleoptera, Diptera, Annelida, Gastropoda, Dermaptera, Heteroptera, Homoptera, Lepidoptera and Archaeognatha. The differences observed between the control and predator excluded plots were principally due the Orthoptera and Blattaria group and Araneae which showed significant suppression in the presence of vertebrate predators (Table 1). Hymenoptera, Isoptera and Myriapoda populations were also lower in control plots, but these differences were not significant (Table 1).

Spiders showed the strongest response of all macro-invertebrate taxa to predator exclusion; they were 2.3 times more abundant in the exclosure sites (Table 1). Most of this response was due to an increase in the jumping spiders (Salticidae). Proportional increases in spider densities relative to other macro-invertebrates in exclosure subplots resulted in a shift in invertebrate guild structure.

Despite increases in the predatory guild of spiders, herbivorous/omnivorous taxa were, on average, 44% higher when vertebrate predators were excluded (split-plot ANOVA on averaged monthly means, $F_{1,6} = 9.99$, p = 0.02). When the detritivorous taxa (fragmenters/consumers of leaf litter) were examined as a group, no significant difference in densities was found among treatments (split-plot ANOVA on averaged monthly means, $F_{1,6} = 1.84$, p = 0.224).

Earthworms averaged 20.2 per m^2 in the top 10 cm of soil of control sub-plots. Exclusion of vertebrates for eight months resulted in earthworm density of over 40.6 per m^2. This difference was significant ($F_{1,6} = 21.27$, p = 0.004), showing the same direction of change as macro-invertebrates of the leaf litter (Fig. 1b).

The most common orders of micro-invertebrates (<5 mm) included Collembola, Acarina, Diptera (primarily fungal gnats, sciarids) and Hymenoptera, which made up 92% of the total sample. Most were too small to be eaten by mammalian or avian insectivores excluded from the fenced plots. They exhibited the opposite trend of macro-invertebrates (Fig. 1b) and were significantly more abundant in control subplots than in fenced areas ($F_{1,4} = 11.22$, p = 0.029). Vertebrate exclusion resulted in an average depression of abundance of 26% ± 18 for micro-invertebrates. Micro-invertebrates classified as the microbivore guild (feeding on soil fungi and bacteria) were made up primarily of Collembola and Acarina species (Takeda and Ichimura 1983). This guild was found as a group to be significantly more abundant in subplots open to vertebrate predators ($F_{1,4} = 9.371$, p = 0.038).

Herbivory

Despite the low incidence of strictly herbivorous taxa and low overall density of invertebrates on the forest floor in general, exclusion of insectivores resulted in an increase of seedling herbivory rates by an order of 4.3 times that of control areas (Fig. 2). The 11.3% rate of seedling herbivory
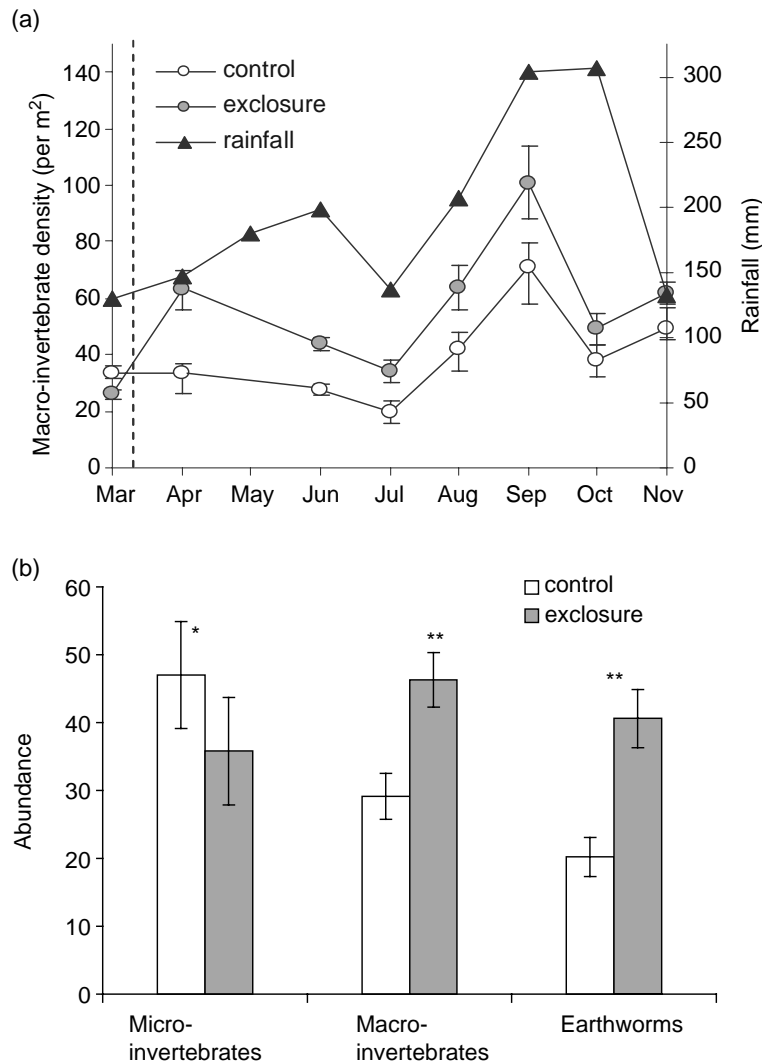
Fig. 1. (a). Effect of exclosure on invertebrate population of forest floor. Dotted line indicates beginning of the experiment. Error bars represent standard error of samples. Pearson's correlation coefficient of treatments $=0.872$, $p=0.005$. (b) Differences in invertebrate abundances summed over all subplots between control and exclosure treatments at the end of eight months of exclosure. Different invertebrate groups should not be compared in magnitude with each other as each uses a different method of sampling. Micro-invertebrates are those <5 mm caught with sticky traps. Large invertebrates are those >5 mm found during direct search. Earthworm numbers are per m^2 in the top 10 cm of soil. Error bars represent standard error. *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$ (single factorial ANOVA adjusted for block effect).

(average percent leaf area consumed/month) by insects observed in exclosure subplots was significantly higher than the 2.6% observed in controls ($F_{1,6}=10.374$, $p=0.018$). When total seedling herbivory was examined (including herbivory by mammalian herbivores) there was still 1.2 times more herbivory in fenced areas but this difference was only marginally insignificant ($F_{1,6}=5.09$, $p=0.065$). Mortality of marked seedlings afflicted by severe invertebrate damage was 2.2 times higher in vertebrate exclosure sites than controls, but this difference was not significant ($F_{1,6}=0.184$, $p=0.223$). This invites future examination with larger sample sizes and extended sampling times.

Nutrients and litter fragmentation

Results did not reveal any difference in leaf litter fragmentation rates between treatments ($F_{1,6}=2.716$, $p=0.150$).

However, inorganic P (plant extractable P) was 1.2 times higher in control subplots than exclosure subplots (Fig. 3a; $F_{1,6}=6.98$, $p=0.038$). Ratios of C:P in the soil were 1.13 times lower in exclosure treatments but the difference was not significant ($F_{1,6}=3.936$, $p=0.094$). No difference was exhibited between treatments for the values of inorganic N (NO_3 and NH_4) (Fig. 3b; $F_{1,6}=0.849$, $p=0.392$) or in ratios of C:N ($F_{1,6}=0.003$, $p=0.957$).

Discussion

There have recently been several studies examining the mechanisms underlying extinction of terrestrial insectivorous species from forest fragments (reviewed by Sekercioglu et al. 2001). This study provides some insight into the possible consequences of such losses. Excluding terrestrial,

Table 1. Effects of exclosure on densities of invertebrate taxa using a split-plot ANOVA with treatment as the main effect. Also presented is the percentage each taxa represented of the total sample and factor differences between treatments. Factor differences were calculated as the mean of overall means in predator exclosure subplots divided by the mean of overall means in control subplots.

Major taxa	% of sample	Mean density (m^2)		Factor difference	Split plot Anova§	
		Open	Exclosure		$F_{1,6}$	p
Orthoptera and Blattaria	33.3	12.79	19.10	1.49	5.29	0.021*
Isopoda	27.8	10.56	16.03	1.52	2.49	0.141
Araneae	11.5	3.37	7.62	2.26	28.83	0.002*
Myriapoda	5.7	2.59	2.86	1.36	0.81	0.447
Hymenoptera	7.4	3.02	4.03	1.33	0.94	0.383
Isoptera	9.1	3.67	5.01	1.11	1.72	0.136

§ significance is for exclosure effect on each group.
*significant after the sequential Bonferroni adjustment.

insectivorous mammals and birds in this study, resulted in significant changes in invertebrate community structure as well as increased levels of seedling herbivory rates and altered nutrient levels on the forest floor. The exclosure treatment resulted in increased macro-invertebrate (>5 mm) densities with the strongest effects on herbivorous taxa, spiders, and earthworms. Numbers of microbivores including Collembolla, Acarina and Sciaridae were negatively affected by exclosure fencing. Herbivory of seedlings was higher and inorganic phosphorus levels were lower in exclosure than in control treatments.

Possible trophic effects involving seedling herbivory

In the above ground grazing web, the most obvious explanation for increased insect herbivory in exclosure plots is that mammalian and avian terrestrial insectivores directly control densities of understory invertebrate herbivores through predation. Another possible cause is that the fencing, which also excludes mammalian herbivores, had caused plants of the forest floor to invest less in structural defenses, which increases palatability to invertebrates (Shimazaki and Miyashita 2002). This is less likely to be the cause of the pattern shown in the present study because the seedlings monitored were small enough that mammalian herbivory always resulted in mortality of the plant (i.e. palatability after mammalian herbivory was not an issue), and seedlings made up most of the live leaf material
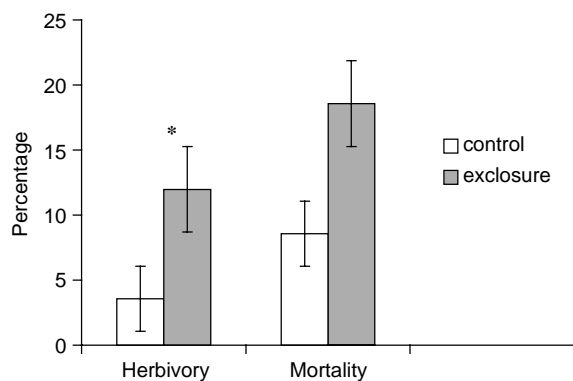
contained within the plots below the 80 cm fencing. There was a higher total herbivory rate in exclosure plots when mammalian herbivory was included in the analysis but this result was not significant ($F_{1,6} = 5.53$, p = 0.277), however, this means that herbivores were not attracted to higher availability of leaf material in exclosure plots. The more parsimonious explanation of these two hypotheses is that excluding predators reduced predation on herbivorous insects resulting in higher densities of herbivores and increases in seedling herbivory.

In contrast to this study, work by Van Bael et al. (2003) found that neotropical birds controlled herbivores in the canopy but not in the understory. Their study, however, involved saplings in forest edge habitat, an environment that is often avoided by understory birds of tropical
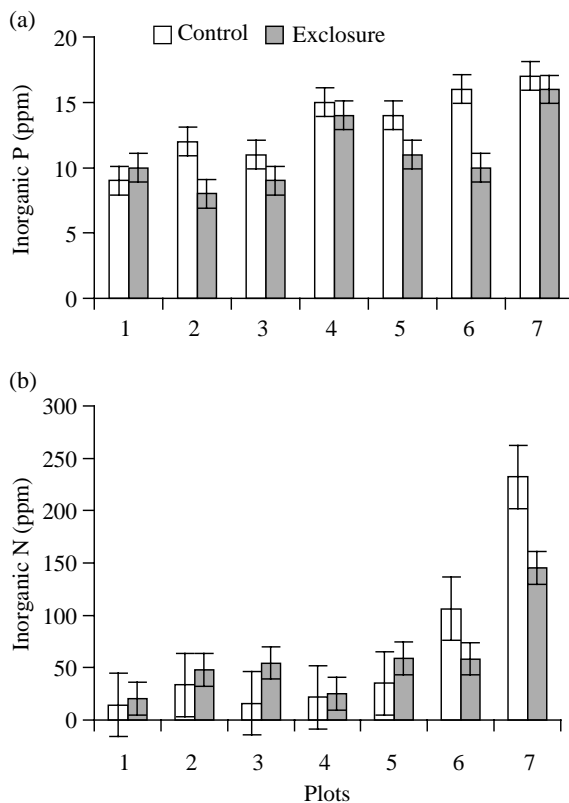
Fig. 3. Extractable phosphorus (a) and extractable nitrogen (b) in control and exclosure subplots after eight months of excluding terrestrial insectivores. Vertical lines indicate standard errors.

Fig. 2. Effects of insectivore exclosure on average percent loss of leaf area and percent mortality of seedlings due to insect herbivory. Error bars represent ±1 SE. * indicates significant difference.

rainforest (Laurance 2004). Saplings also face different pressures and communities of organisms than seedlings close to the forest floor. Perfecto et al. (2004) however, found that insectivorous birds in neotropical coffee plantations with more forest structure and plant diversity have higher impact on understory herbivores, presumably because the insectivorous birds exist at greater densities there.

The results of the present study support the notion that mammals and birds preying upon invertebrates are likely to provide an important ecosystem service by eating invertebrate pests (Sekercioglu et al. 2004, Sekercioglu 2006). It has been suggested that the more fragmented or degraded the forest system, the higher the risk of pest outbreak may be in surrounding systems (Dent 1991, Roland 1993). Some authors have suggested that this pattern might be linked to the declines of terrestrial insectivorous vertebrates in fragmented forests (Watt et al. 1997, Sekercioglu 2002). Seedling herbivory may also be one mechanism for slower forest regeneration often observed in forest patches where diversity and abundance of this functional group is often compromised (Terborgh et al. 2001). Evidence directly linking herbivory as a mechanism to decreased seedling survivorship in fragmented forest is limited, however, Benitez-Malvido (2002) found that herbivory of shade-tolerant tree seedlings transplanted to fragments in Brazil, increased with decreasing fragment size (Urbas et al. 2007). Further observational studies examining invertebrate community structure and experimental transplant studies to evaluate levels of herbivory and relative impact of insectivores in fragmented and intact forests will be useful.

Possible trophic cascades affecting soil nutrients

The strong effect of exclosure fencing on inorganic phosphorus levels observed in the experiments could have been caused by top down cascades involving trophic and/or behaviorally mediated interactions, or through bottom up effects caused by excluding solid and liquid waste material normally deposited by vertebrates (Wyman 1998, Beard et al. 2003). Data from the experiment was used in path analyses to evaluate these two hypotheses and to decipher likely scenarios and possible direct and indirect interactions in the community.

The top down cascade hypothesis requires that the higher microbivore densities in the treatments exposed to terrestrial mammals and birds caused higher levels of inorganic P levels available in the soil. Higher rates of microbivore grazing on fungal and bacterial communities can increase microbial production and the release of P from microbial tissues (Mikola and Setälä 1998). Nutrients are released from the arthropods by excretion or following the death of the animals. This can result in increased mobilization of inorganic P, a form extractable by plant roots (Lussenhop 1992). In this scenario, microbivores may have responded directly to changes in spider densities (as in Lawrence and Wise 2000), which were higher in exclosure plots or they may have responded to changes in spider foraging behavior in the presence or absence of vertebrate predators (behaviorally mediated effect). In a top-down system, spider densities could have been higher in exclosure

subplots because of reduced predation and/or reduced competition for macro-invertebrate prey.

Data from the experiment was used to evaluate and eliminate some of these possible scenarios through a path analysis. The top down scenario most supported by the analysis was a four level trophic cascade in which mammalian and avian insectivore presence negatively affects spiders, which leads to more microbivores, which positively affects inorganic P levels in the soil (Fig. 4). This result was surprising for a system in which prey have many refugia in a structurally complex environment such as the leaf litter in this study. A behaviorally mediated indirect effect of vertebrate insectivores on microbivores could not be ruled out and would be difficult to discern from this path analysis. However, given the sporadic occurrence of vertebrate predators, the effect of their presence on behavioral changes in spiders seems unlikely to be driving the patters observed.

The path analysis also suggested that reduction of competition for invertebrates was unlikely to be driving increases in spider densities in exclosure subplots because there was a significant negative interaction between spiders and non-predatory macro-invertebrate prey. However, the strength of interactions produced by the path analysis and the higher densities of macro-invertebrates in exclosure plots suggests that vertebrate predators excluded in this experiment were more important than spiders in affecting densities of macro-invertebrates inhabiting the forest floor.

Previous work in the neotropics has suggested that nutrient ratios in the soil can cause variation in the density of the microbivorous fauna, with total C:P ratios negatively correlating with microbivore densities (McGlynn et al. 2007). Thus an alternative hypothesis for altered
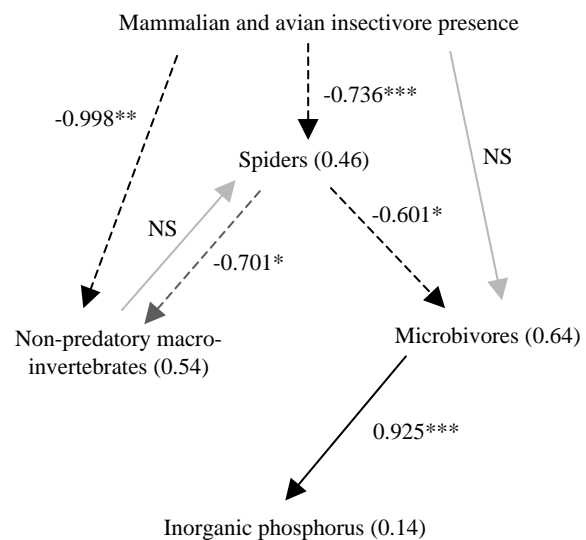
Fig. 4. Results of a path analysis evaluating the effects of excluding mammalian and avian terrestrial insectivores on soil inorganic phosphorus. In the interaction web, arrows designate the direction of causality hypothesized. Solid lines represent positive effects and dashed lines represent negative effects. Non-significant paths are omitted. Numbers adjacent to arrows represent the size of the effect on abundance (path coefficients). Numbers between parentheses next to endogenous variables represent the proportion of variance unexplained by the model (error variance). AIC for the model equals 38.79.

microbivore densities is a bottom-up scenario (i.e. driven by resource quality) in which exclusion of nutrient deposit by terrestrial mammals and birds in exclosure sites may have resulted in higher C:P soil ratios and lower collembolan densities. A path analysis was used again to distinguish whether this hypothesis was more or less likely than the top-down hypothesis discussed previously. The soil C:P ratios were not significantly higher in exclosure plots and results of the path analysis lead to a rejection of all interaction links implied by this bottom up scenario (Fig. 5). This suggests that nutrient addition by terrestrial mammals and birds is unlikely to be driving the pattern of nutrient ratios or invertebrate densities observed in the experiment. Average C:P ratios in plots also did not vary with the magnitude of exclosure treatment effect on microbivore abundance (Pearson's $r = 0.395$, $F = 1.955$, $p = 0.256$) suggesting that site-specific stoichiometry is not affecting the strength of the top down trophic cascades in this system. Since these relationships were only examined at the end of the experiment, it is unclear if top down effects on the soil web are important during all seasons and further work in this area is needed.

Results presented here suggest that understory insectivores are an important link in terrestrial food webs and nutrient cycling. This contradicts the general view that large bodied predators must have low potential for affecting forest floor food webs due to their proportionally low biomass and turnover in the forest (Setälä et al. 1998). If this trophic effect is common to other systems, loss of these species may partially explain lower levels of nutrient turnover found in fragmented forests (Didham 1998). This relationship might be stronger in tropical regions, where climatic influences are less important for decomposition rates than biological regulation by soil fauna (González

and Seastedt 2001). This experiment suggests that exclusion of vertebrate insectivores negatively affects levels of plant extractable P, one of the most limiting nutrients in tropical forests for plant growth. Phosphorus has been shown to limit not only plant growth, but decomposition of organic carbon in tropical systems by restricting microbial productivity (Cleveland et al. 2002). Therefore, factors influencing P levels have profound implications for primary productivity and carbon cycling in moist tropical forests. The consequences of altered inorganic P levels on seedling growth and herbivory caused by exclusion of terrestrial avian and mammalian insectivores were not examined here, but may be interesting for further research.

Implications of results

Changes in invertebrate densities in this study were very localized and, in some cases, likely due to altered immigration or emigration within the study plots and do not necessarily represent population change through altered survival. I suggest that loss of terrestrial insectivores from an entire forest is likely to be correlated with similar patterns of change, but may occur at different magnitudes and time scales than observed in this study. Thus, future studies encompassing larger spatial and temporal scales will be important to discern the relative importance of these potentially strong trophic interactions at regional scales.

This work supports previous empirical work in other systems where insectivorous vertebrates have been shown to not only influence herbivores and their host plants (reviewed by Halaj and Wise 2001), but can also influence detrital web processes through the effects of aboveground cascades on soil food webs (Wardle et al. 2005, Fukami et al. 2006). The complexity of the rainforest floor did not infer resistance to perturbations in trophic diversity, and even below ground processes were affected, despite the added structural heterogeneity of the leaf litter. This study suggests that vertebrates may play an important role in both above and below ground food webs of the forest floor. Their role should be considered in both our understanding of terrestrial food-web ecology, as well as for conservation and management of ecosystem functioning and services.
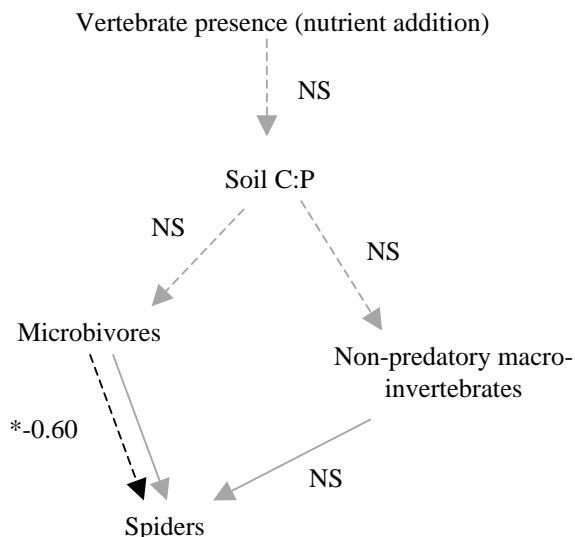
Fig. 5. Hypothesized interaction web displaying bottom-up effects of excluding vertebrates on nutrients and invertebrate abundances. The meaning of arrows and numbers are described in Fig. 4. In this path diagram, gray lines indicate hypothesized interactions that were rejected through path analysis because either the interaction was not significant (NS) or the sign of that interaction is the opposite of that predicted (black lines indicate significant interactions).

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