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# Top-down effects of a terrestrial frog on forest nutrient dynamics

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**Abstract** Many studies have found top-down effects of predators on prey, but few studies have linked top-down effects of vertebrate predators to nutrient cycling rates in terrestrial systems. In this study, large and significant effects of a terrestrial frog, *Eleutherodactylus coqui* (coquí), were recorded on nutrient concentrations and fluxes in a subtropical wet forest. In a manipulative experiment, coquís at natural densities were contained in or excluded from 1 $m^3$ enclosures for 4 months. Chemistry of leaf wash (throughfall), foliage, and decomposed leaf litter in the enclosures were measured as indicators of coquí effects on nutrient cycling. Coquí exclusion decreased elemental concentrations in leaf washes by 83% for dissolved organic C, 71% for $NH_4^+$, 33% for $NO_3^-$, 60% for dissolved organic N, and between 60 and 100% for Ca, Fe, Mg, Mn, P, K, and Zn. Coquí exclusion had no effect on foliar chemistry of plants transplanted into the enclosures. However, coquí exclusion decreased nutrient availability in decomposing mixed leaf litter by 12% and 14% for K and P, respectively, and increased C:N ratios by 13%. Changes in nutrient concentrations that occurred with coquí exclusion appear to be due to concentrations of nutrients in coquí waste products and population turnover. The results supported our hypothesis that coquís have an observable effect on nutrient dynamics in this forest. We suggest that the primary mechanism through which they have this effect is through the conversion of insects into nutrient forms that are more readily available for microbes and plants. The potential for higher trophic level species to affect nutrient cycling through this mechanism should not be overlooked.

**Keywords** Amphibians · Decomposition · Enclosures · Nutrient cycling · Puerto Rico

## Introduction

Research determining the role of single species in terrestrial ecosystem processes continues to be a high research priority because of the importance of maintaining functioning ecosystems (Daily 2000), the predictions of increased species losses globally (Chapin et al. 2000), and the increased awareness of invasive species and their ecosystem impacts (Vitousek et al. 1996). Determining the ecosystem level effects of losing vertebrate predators in terrestrial ecosystems is of particular importance because these species are often the most threatened with extinction (Pimm et al. 1988). Recent studies have revealed that predators not only have top-down trophic cascading effects on their prey in simple or aquatic systems, but also in diverse terrestrial ecosystems (Dial and Roughgarden 1995; Letourneau and Dyer 1998; Terborgh et al. 2001). While our understanding of the role of vertebrate predators in controlling their prey in terrestrial systems is growing (Hunter 2001a), our understanding of their role in increasing nutrient cycling rates by increasing nutrient availability is much less developed.

As a generality, vertebrate predators are considered to represent too little biomass and, as a result, productivity to regulate nutrient availability at the ecosystem level in terrestrial systems (Schlesinger 1997). However, biomass is not a sufficient indicator of ecological importance in nutrient cycles because it does not provide information on two important fluxes of nutrients through organisms: waste material production and population turnover (i.e., carcasses). The importance of these fluxes can be greater than would be expected based on their quantities because

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increased nutrient availability can produce positive, nonlinear growth responses in microbial communities (Hanlon 1981; Visser 1985), and essential nutrients delivered in pulses can be important in maintaining ecosystem functioning (Lodge et al. 1994). While it is well known that all animals return a substantial portion of the nutrients they consume back to the detrital system in the form of concentrated, highly labile liquid and solid wastes, and corpses (Ruess and McNaughton 1987), the research that has been conducted in this area is typically focused on herbivore and, in particular, insect (Hunter 2001b), and decomposer populations (Hanlon 1980; Teuben and Verhoef 1992). The potential for vertebrate predators to influence nutrient pools and fluxes through these mechanisms remains relatively unexplored.

The studies that have been done on single faunal species effects on nutrient cycling from waste material and carcasses show heterogeneous effects on the ecosystem level. For example, studies have measured the effects of such organisms as roosting birds and ungulates, which have spatially heterogeneous influences on nutrient influx from waste material (Gilmore et al. 1984; Frank et al. 1994). The studies that have been conducted on decomposing carcasses often show temporally heterogeneous effects (e.g., in “outbreak” situations; Swank et al. 1981; Schowalter and Crossley 1983; Parmeter and Lamarra 1991; Wipfli et al. 1998). Waste and carcass effects are thought to occur more quickly than changes induced by litter quality, canopy cover, and community composition (McNaughton et al. 1988). However, it is the ‘slower’ variety of effects in terrestrial systems (e.g., changes in plant community composition) that often show the effects of faunal species on nutrient cycling homogeneously at the whole-system level (Brown and Heske 1990).

Island ecosystems offer a unique opportunity to analyze top-down effects of predators on nutrient cycling because few species exist at each trophic level and species population densities are typically high. Caribbean islands are ideal for studying the role of amphibians in nutrient cycling because they are present in unusually high densities. We decided that an amphibian was an appropriate organism for this study because amphibians have been noted for their population extinctions and global declines (Richards et al. 1993; Lips 1998), and their experimental exclusion represents their potential loss from the system. Although research has been conducted to document the causes and extent of amphibian loss, few studies have examined how changes in their population levels might affect nutrient cycling. The studies that have examined the effects of amphibians on nutrient cycles have not investigated the role of their waste materials and carcasses (e.g., Seale 1980; Wyman 1998; Kiffney and Richardson 2001).

The terrestrial frog, *Eleutherodactylus coqui* (coquí), a species endemic to Puerto Rico, has one of the highest population densities ever recorded for terrestrial amphibians (average density of 20,000 individuals ha$^{-1}$) and represents the greatest biomass of any single vertebrate species in the subtropical wet forests it inhabits (Stewart and Woolbright 1996). The study system has higher insectivore density and lower insect diversity than comparable continental areas (Garrison and Willig 1996; Angulo-Sandoval and Aide 2000). Coquís have been estimated to consume 114,000-prey items ha$^{-1}$ night$^{-1}$ in the study forest (Stewart and Woolbright 1996). In addition, coquís have been found to alter the study forest by reducing arthropod numbers, reducing herbivory rates, increasing plant net primary production, and increasing leaf litter decomposition rates (Beard et al., in review). We thought that this amphibian, if any, was likely to affect nutrient cycling by increasing nutrient availability at the ecosystem level.

For this research, we determined whether an insectivore, the coquí, has measurable effects on nutrient concentrations and fluxes in the subtropical wet forests of Puerto Rico. We hypothesized that deposition of labile forms of nutrient-rich wastes by territorial coquís would result in detectable shifts in N, P, and K fluxes. Since these nutrients are the same nutrients that regulate plant growth and decomposition in this forest (Silver et al. 1994), we hypothesized that coquís help alleviate nutrient deficiencies at the plant and decomposer levels. We tested three specific hypotheses: (1) primary producers acquire essential nutrients from coquís as excrement deposited on plant surfaces become part of ecosystem fluxes of nutrients (e.g., throughfall), (2) coquí deposition of nutrients on plant surfaces changes foliar chemistry and nutrient absorption directly at the leaf level (Boyce et al. 1996), and (3) the pulsed addition of labile, nutrient-rich waste to soil could change decomposition rates since microbial activity levels are controlled by the availability of limiting nutrients (Anderson and Swift 1983). To place our findings in a broader context, we quantified the amount of nutrients in coquís, the amount of nutrients eliminated and excreted, and the amount of nutrients cycled through the population.

## Materials and methods

### Study site

The research site was located in the Luquillo Experimental Forest (LEF), which is classified as subtropical wet forest, in the northeastern corner of Puerto Rico (18°18'N, 65°50'W). Mean monthly air temperatures average between 21 and 24°C throughout the year (Garcia-Martino et al. 1996). Peak precipitation (inputs average 400 mm month$^{-1}$) occurs from May to November, with drier periods recorded between January and April (inputs average 200–250 mm month$^{-1}$) (Garcia-Martino et al. 1996). Average annual precipitation is 3,537 mm year$^{-1}$ (Garcia-Martino et al. 1996). The experiment was conducted during the wet season from June through October 1999, when the annual precipitation was 3,746 mm year$^{-1}$ (F.N. Scatena, unpublished data) and average inputs were 342 mm month$^{-1}$ (F.N. Scatena, unpublished data).

The study site was located in the mature secondary Tabonuco forest zone that is dominated by *Dacryodes excelsa* (tabonuco), *Prestoea montana*, *Sloanea berteriana*, and *Cecropia schreberiana*. The understory was dominated by *Danea nodosa*, *Ichnanthus palens*, *Heliconia carabea*, *Piper glabrescens*, *Pilea inegualis*, *Prestoea montana*, and *Scleria canescens*. The experiment was conducted in a 30×35-m area, at an elevation of 250 m, in the Bisley Experimental Watersheds.

Hurricane Hugo passed through Puerto Rico in September 1989, and Hurricane Georges passed through Puerto Rico in September 1998. Both the intensity and damage of Hurricane Georges was less than that associated with Hugo in the study forest (Ostertag et al. 2002). For example, after Hurricane Georges, litter floor mass, and nutrient dynamics returned to pre-hurricane levels in 4–5 months, whereas these ecosystem components took over 5 years to return after Hugo (Ostertag et al. 2002). Foliage levels returned within 2 months following Georges (F.N. Scatena, unpublished data). Prior to the initiation of this experiment, measured ecosystem stocks and processes had returned to pre-hurricane levels.

### Experimental design

Twenty field enclosures 1 $m^3$ in size were constructed using a frame of PVC plastic tubing covered by plastic mesh material with 0.95×0.95 cm (3/8×3/8 inch) mesh size openings. This mesh size opening was chosen because it was large enough to allow free movement of most invertebrates into and out of the container but small enough to prevent the movement of adult coquís. Juvenile coquís could enter through this mesh size. Enclosures were monitored weekly at night. Juveniles were observed in enclosures on two occasions and *Anolis* lizards on one occasion and were subsequently removed. No other vertebrates were observed in the enclosures.

All enclosures were placed in pairs directly on the surface of the forest floor. One enclosure in each pair contained no coquís and the other contained coquís at a high-end estimate of natural densities (7 adult coquís $m^{-2}$). This number was determined using the maximum estimate recorded for adults of 1.14 individuals $m^{-2}$ prior to Hurricane Hugo passing through the island of Puerto Rico in 1989 (Stewart and Woolbright 1996) and the 6-fold increase in the adult population density after the hurricane (Woolbright 1996). When mortality was observed in enclosures, carcasses were not removed, and frogs were replaced to keep the density constant throughout the experiment. Adult survivorship in enclosures was 86% during the study period.

To standardize the testing of coquí impacts on foliage chemistry, *Piper glabrescens* (Piperaceae) plants and *Manilkara bidentata* (Sapotaceae) seedlings were transplanted into pots for placement within each enclosure. Four replicate plants per species were transplanted into 18-cm diameter pots for placement in each enclosure. *Piper* was selected because it is a common understory shrub species and *Manilkara* because it is a common tree species found in this forest. Plants used in the experiments were excavated from the forest area immediately surrounding the study area and transplanted into the pots using soil from the site. Potted plants were allowed to equilibrate at the field sites for several weeks prior to their placement into the enclosures and were randomly selected for placement into enclosures.

### Throughfall

To determine how coquís affect throughfall water chemistry, 'leaf washes' were obtained using methods articulated in Rea et al. (2000). Two separate samples were collected from each enclosure: one sample a composite collection from four *Manilkara* seedlings and the other sample a composite collection from the four *Piper* plants that were placed inside each enclosure. For each sample, plants had distilled water sprayed over the top of each leaf on each plant. A funnel was used to collect the leachates. A total of 60 ml was collected from each species at each sampling time. Leaf wash samples were collected every 2 weeks over the 4-month study period. Leaf wash samples were stored in a freezer until they were analyzed. All samples were filtered through GF/A glass fiber filters (Whatman) prior to chemical analyses.

Total organic carbon (TOC) was measured using a TOC analyzer (Shimadzu TOC-5000A). With filtered samples, the TOC analyzer measures dissolved organic carbon (DOC). Dissolved inorganic nitrogen (ammonium, $NH_4^+$-N, and nitrate, $NO_3^-$-N) was determined using a Perstop flow analyzer, and cations were analyzed using a Perkin Elmer inductively coupled plasma optical emission spectrophotometer (ICP-OES). Total dissolved nitrogen was measured in samples following an alkaline persulfate digestion with digests subsequently analyzed for $NO_3^-$ using the flow analyzer automated colorimetric nitrate analysis. Dissolved organic nitrogen (DON) was estimated by subtracting dissolved inorganic N from total dissolved N. Chemical analyses for DOC, DON, and cations on the ICP-OES were conducted on samples collected during the last seven sampling periods and on $NH_4^+$-N and $NO_3^-$-N for eight sampling periods.

### Foliage

To determine and quantify whether coquís affect the chemical quality of plant foliage, equal weight leaf samples were collected from each plant and were combined to produce one sample per species (*Piper* and *Manilkara*) per enclosure. Similar samples were collected from plants that remained outside the enclosures. Samples composited by species for each enclosure were oven-dried at 70°C and ground using a Wiley Mill with a number 20 (2 mm) mesh screen. Total C and N concentrations in foliage were determined by dry combustion using the CHN elemental analyzer (LECO CNH-600). Foliage elemental concentrations of Al, Ca, Fe, Mg, Mn, P, K, and Zn were analyzed using a digestion procedure outlined in Friedland et al. (1984). As part of this method, samples were ashed at 500°C overnight in a muffle furnace and digested in 6 N $HNO_3$. The digests were then analyzed using the ICP-OES.

### Leaf litter

To determine and quantify whether coquís change the nutrient concentrations of recently senesced leaf tissues during decomposition, two litterbags (15 ×15 cm in size) were placed in each enclosure (Anderson and Swift 1983). Each litterbag was constructed of fiberglass mesh material with 2-mm size openings and was filled with 5 g of air-dried leaf litter (air-dried for >24 h). Recently senesced litterfall was collected from the forest floor near the study site. The mixed leaf samples consisted of the dominant plant species in the site *Dacryodes excelsa*, *Sloanea berteriana*, *Cecropia schreberiana, Piper glabrescens*, *Manilkara bidentata, Psychotria berteriana*, *Palicourea riparia*, and *Miconia* spp. Subsamples of air-dried litter were collected at the same time that litterbags were being constructed and used to produce an air-dried to oven-dried conversion factor.

Litterbags were removed at the termination of the experiment (after 4 months). This period of time was deemed appropriate since decomposition rates are <1 year in this forest (Bloomfield et al. 1993). Prior to chemical analyses, each retrieved litterbag was cleaned of surface-adhering material and soil, and the remaining litter material was oven-dried at 70°C. Litter samples were ground using the same methods as the foliage samples. A subsample from each litterbag was ashed overnight at 500°C to develop an ash-free conversion factor to account for mineral contamination. Initial and decomposed leaf litter samples were analyzed for their elemental concentrations (Al, Ca, Cu, Fe, Mg, Mn, P, K, and Zn) using the method outlined in Friedland et al. (1984). Digests were analyzed using the ICP-OES. Total C and N of litter samples were determined using the CHN elemental analyzer.

### Coquís and invertebrates

Frog and invertebrates were collected within 300 m of the study site in September and October 1999. Measurements were made on three typical adult frogs (one female and two males) and three juvenile frogs. Each individual frog was frozen, oven-dried at 70°C until constant weight, and ground. Invertebrates were collected using

Malaise traps and a dry collection technique within 300 m of the study site. Invertebrates were consolidated, oven-dried at 70°C until constant weight, and ground. Total C and N in the frogs and invertebrates were determined using the CHN elemental analyzer. Elemental concentrations of the frogs and invertebrates were analyzed following digestion (Friedland et al. 1984) using the ICP-OES.

### Urine and feces

Urine and feces were sampled from coquís collected between 2000 and 2400 hours within 300 m of the study site in September and October 1999. Frogs were placed in individual plastic bags overnight. The bags contained sufficient air during this period to not adversely affect them. Frogs were contained in the bags from 9–15 h, released, and returned to the forest. These samples provide a conservative estimate of how much urine and feces coquís produce nightly since frogs had just emerged from retreats and had not foraged.

To collect excrement, 60 ml of distilled water was added to each plastic bag and mixed thoroughly. The 60 ml of water and urine were then immediately frozen in small vials. To create control vials, 60 ml of distilled water was rinsed in plastic bags, transferred to vials, and frozen. All samples were filtered before they were analyzed. There were 28 urine and 28 control samples for the urine analysis. Coquí fecal material consists of discrete pellets. When fecal matter was present, it was removed from the plastic bags before the urine was rinsed out, placed in vials, and frozen. Two samples of 30 consolidated fecal pellets were analyzed separately for the feces analyses. Averages of the two samples are presented. All samples were stored frozen until analyzed. Coquí urine was analyzed for DOC using the TOC analyzer, $NH_4^+$-N, $NO_3^-$-N, and DON using the flow analyzer, and cations using the ICP-OES. Coquí feces were analyzed for total C and N using the CHN elemental analyzer and cations using the ICP-OES.

### Statistical analyses

All statistical analyses were conducted using SAS for Windows (6.12). To determine differences between the 10 experimental enclosures and 10 control enclosures and differences between the 28 urine and 28 control samples, *t*-tests for two independent samples were conducted using the TTEST procedure (SAS 1990). For some throughfall analyses, where sampling dates served as replicates, *t*-tests for paired means were conducted using the MEANS procedure (SAS 1990). Averages for the variables were calculated for each enclosure or each date as appropriate. Assumptions of normality were met when necessary with log-transformations.

## Results

### Throughfall

Leaf wash DOC concentrations were significantly greater in the presence of coquís on two of seven sampling dates for both *Piper* and *Manilkara* ($df$=18, $P$<0.05). Leaf wash DON concentrations were significantly greater in the presence of coquís on three of seven sampling dates for *Piper* and two of seven sampling dates for *Manilkara* ($df$=18, $P$<0.05). Leaf wash $NH_4^+$ concentrations were significantly greater in the presence of coquís on one of eight sampling dates for *Piper* and on two of eight sampling dates for *Manilkara* ($df$=18, $P$<0.05). Leaf wash $NO_3^-$ concentrations were significantly greater in the presence of coquís on one of eight sampling dates for *Piper* and on two of eight sampling dates for *Manilkara* ($df$=18, $P$<0.05). Ca, Fe, Mg, Mn, P, and K were found to be significantly greater in the presence of coquís on at least one of seven sampling dates for at least one of the plant species ($df$=18, $P$<0.05). Al and Zn were the only elements that were not found to be significantly greater in the presence of coquís on at least one of seven sampling dates ($df$=18, $P$>0.05). Elemental concentrations in leaf washes with all sampling dates included are listed in Table 1.

### Foliage

No differences were recorded in the foliar concentrations of total C, total N, or their C:N ratio when comparing *Piper* plants or *Manilkara* seedlings growing in enclosures with or without coquís ($df$=18, $P$>0.05). There were no differences in foliar elemental concentrations of Al, Ca, Cu, Fe, Pb, Mg, Mn, P, K, and Zn when comparing *Piper* or *Manilkara* growing in enclosures with and without coquís ($df$=18, $P$>0.05). There were no differences between the plants placed in the enclosures and the plants that remained outside the enclosures ($df$=38, $P$>0.05).

**Table 1** Mean elemental concentrations in mg $L^{-1}$ (±1 SE) in leaf washes collected biweekly from June to October 1999 in enclosures with coquís at post-disturbance densities and without coquís in the Bisley Watersheds, Luquillo Experimental Forest, Puerto Rico. *Effect* was determined as the percent change in concentrations in leaf washes collected as a result of coquí exclusion and was calculated as the percent change in the variable: (without coquis – with coquis) / (with coquis); *DOC* dissolved organic carbon; *DON* dissolved organic nitrogen

| Element | *Piper* | | | *Manilkara* | | |
|---|---|---|---|---|---|---|
| | Coquís | No coquís | Effect | Coquís | No coquís | Effect |
| DOC | 12.62±7.55 | 1.52±0.34 | –88% | 6.02±3.23 | 1.35±0.34 | –78% |
| DON | 0.61±0.90 | 0.35±0.16* | –43% | 1.50±0.47 | 0.34±0.09* | –77% |
| $NH_4^+$ | 1.50±0.47 | 0.34±0.09* | –75% | 0.58±0.23 | 0.19±0.09* | –67% |
| $NO_3^-$ | 0.17±0.11 | 0.04±0.01 | –76% | 0.09±0.03 | 0.10±0.08 | +11% |
| Al | 0.017±0.01 | 0.014±0.00 | –18% | 0.017±0.00 | 0.021±0.01 | +24% |
| Ca | 1.87±0.77 | 0.70±0.14* | –63% | 0.78±0.34 | 0.33±0.03* | –58% |
| Fe | 0.28±0.27 | 0.010±0.00* | –96% | 0.14±0.13 | 0.02±0.01 | –88% |
| Mg | 0.20±0.08 | 0.086±0.02* | –58% | 0.078±0.02 | 0.04±0.01* | –49% |
| Mn | 0.12±0.11 | 0.003±0.00* | –97% | 0.055±0.05 | 0.005±0.00* | –90% |
| P | 8.62±8.52 | 0.55±0.54* | –94% | 0.98±0.67 | 0.065±0.03* | –93% |
| K | 22.22±21.67 | 0.34±0.06* | –98% | 10.38±10.13 | 0.89±0.74* | –91% |
| Zn | 0.12±0.12 | 0.00±0.00 | –100% | 0.051±0.05 | 0.00±0.00 | –100% |

* There were significant differences when making comparisons by element between treatments for that plant species using a *t*-test at $P$=0.05

**Table 2** Mean elemental concentrations of leaf litter in g kg$^{-1}$ (±1 SE) after decomposing for 4 months in enclosures with coquís at post-disturbance densities and without coquís in the Bisley Watersheds, Luquillo Experimental Forest, Puerto Rico

| Element | Enclosures with coquís | Enclosures with no coquís |
|---|---|---|
| C (g kg$^{-1}$) | 385.88±3.14 | 413.72±3.32 |
| N (g kg$^{-1}$) | 14.60±0.01 | 13.69±0.00 |
| C:N ratios | 26.68±0.82 | 30.36±1.00* |
| Al (g kg$^{-1}$) | 12.35±1.61 | 9.69±1.33 |
| Ca (g kg$^{-1}$) | 15.14±0.80 | 15.44±0.92 |
| Cu (g kg$^{-1}$) | 0.02±0.00 | 0.02±0.00 |
| Fe (g kg$^{-1}$) | 9.16±1.20 | 7.25±1.16 |
| K (g kg$^{-1}$) | 1.09±0.04 | 0.95±0.02* |
| Mg (g kg$^{-1}$) | 1.71±0.05 | 1.65±0.04 |
| Mn (g kg$^{-1}$) | 0.78±0.04 | 0.72±0.02 |
| P (g kg$^{-1}$) | 0.61±0.03 | 0.52±0.02* |
| Zn (g kg$^{-1}$) | 0.04±0.00 | 0.04±0.01 |

* There were significant differences when making comparisons by element between treatments using a *t*-test at *P*=0.10

## Leaf litter

After 4 months of mixed leaf litter decomposition, there was no significant difference in the total C or total N contents of the litter by treatment (Table 2). However, the C:N ratio of decomposing leaf litter was lower in enclosures with coquís than in enclosures without coquís (*df*=18, *t*=2.85, *P*=0.01). Differences were recorded in the amount of nutrients measured in decomposing leaf litter collected from enclosures with and without coquís after 4 months (Table 2). Both K and P concentrations were higher in leaf litter collected from enclosures with coquís than without coquís, although the difference was only significant for K (*df*=18, *t*=3.17, 2.14, *P*=0.02, 0.08, respectively). None of the other elements analyzed (Al, Ca, Cu, Fe, Mg, Mn, and Zn) were found to differ significantly between the treatments (*df*=18, *P*>0.05, for all).

## Coquís and invertebrates

Individual coquís analyzed in this study were typical (Stewart and Woolbright 1996). The female dry weight (wt) was 0.97 g [snout-vent length (SVL)=36.9], the males averaged 0.47 g dry wt (SVL=29.55), and the juveniles averaged 0.05 g dry wt (SVL=13.57). On average, coquí tissue consisted of 78.7% water. On a dry wt basis, coquís had the following elemental compositions: 43.9% C, 11.9% N, 5.7 mg kg$^{-1}$ Al, 3,540 mg kg$^{-1}$ Ca, 0.8 mg kg$^{-1}$ Cu, 9.8 mg kg$^{-1}$ Fe, 142 mg kg$^{-1}$ Mg, 1.2 mg kg$^{-1}$ Mn, 2,530 mg kg$^{-1}$ P, 1,020 mg kg$^{-1}$ K, and 8.2 mg kg$^{-1}$ Zn. Coquí elemental concentrations are summarized in kg ha$^{-1}$ in Fig. 1 and Table 3. On a dry wt basis, invertebrate had the following elemental compositions: 48.2% C, 10.6% N, 1,350 mg kg$^{-1}$ Al, 1,680 mg kg$^{-1}$ Ca, 51.7 mg kg$^{-1}$ Cu, 880 mg kg$^{-1}$ Fe, 1,540 mg kg$^{-1}$ Mg, 77 mg kg$^{-1}$ Mn, 9,120 mg kg$^{-1}$ P, 10600 mg kg$^{-1}$ K, and 262 mg kg$^{-1}$ Zn. Invertebrate elemental concentrations are summarized in kg ha$^{-1}$ in Table 1 and Fig. 1.

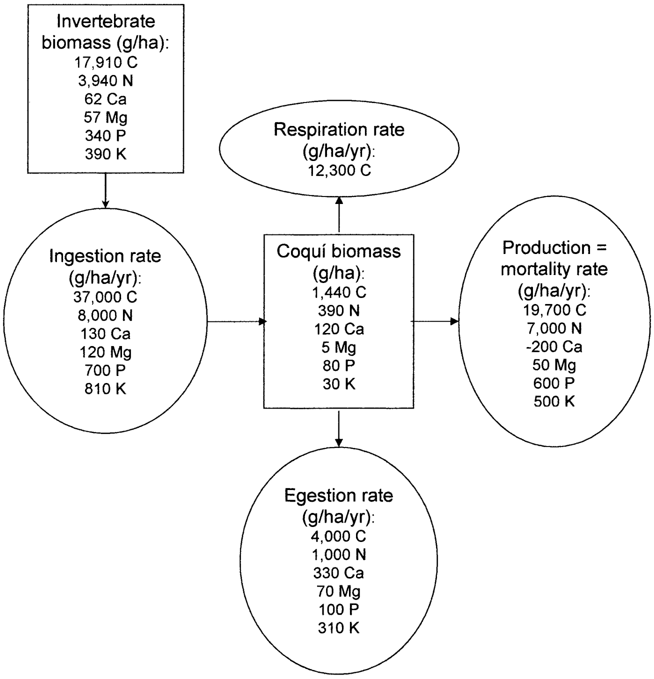

**Fig. 1** Model of nutrients cycling in coquí populations at average densities in the Luquillo Experimental Forest, Puerto Rico. Modeled after Burton and Likens (1975b). Values for ingestion, egestion, and biomass are independent estimates. Coquí respiration and production are dependent estimates and were estimated using parameters from Stewart and Woolbright (1996). The missing Ca source may be from prey items, such as snails, that were not included in the analysis

To determine the elemental content of invertebrates in kg ha$^{-1}$, their elemental content and total dry wt biomass were used (Table 3). To estimate the dry wt of invertebrates consumed by coquís, the total number of individuals consumed, the percent of the total that was each prey item, and prey item dry wt estimates were used. The amount of each element that coquís egest was estimated using an ingestion-egestion coefficient from Woolbright (1985). Egestion was also estimated using the urine and feces results below.

## Urine and feces

Coquí urine contains more $NH_4^+$ than $NO_3^-$ (*df*=27, *P*<0.001). There were higher concentrations of $NH_4^+$ in the urine than in the control samples (*df*=27, *P*<0.001). There was no difference in $NO_3^-$ concentrations between urine and control samples (*df*=27, *P*=0.21). There were greater concentrations of organic N in the urine than in the control samples (*df*=27, *P*<0.001). However, the percentage of total N that was organic did not differ between the urine and control samples, with both urine and control samples averaging 62% organic N (*df*=27, *P*=0.97). There were greater concentrations of DOC in the

**Table 3** The estimated amount of each element in invertebrates as a percent or in mg kg$^{-1}$, and in kg ha$^{-1}$, and the estimated amount of each element in coquí ingestion and egestion in kg ha$^{-1}$ year$^{-1}$ in the Luquillo Experimental Forest, Puerto Rico. Invertebrates and coquís were modeled at average densities. Total invertebrate dry wt biomass was estimated to be 37.2 kg ha$^{-1}$ (Odum et al. 1970). This includes herbivores, decomposers, and spiders, but underestimates total biomass because some prey items (e.g., pseudoscorpions, scorpions, and snails) are not included. Data on the mean biomass of invertebrates consumed by coquís was derived from the total prey items per year and the percent of each prey item consumed from Stewart and Woolbright (1996). The mg dry wt prey item$^{-1}$ is from Reichle (1977). The amount of each element egested by coquís was determined using the ingested-egested conversion factor of 14.45% from Woolbright (1985)

| Element | Elemental concentrations of invertebrates | Elemental content of invertebrates (kg ha$^{-1}$) | Elemental content of coquí ingestion (kg ha$^{-1}$ year$^{-1}$) | Elemental content of coquí egestion (kg ha$^{-1}$ year$^{-1}$) |
|---|---|---|---|---|
| C | 48.2% | 17.91 | 36.96 | 5.37 |
| N | 10.6% | 3.94 | 8.13 | 1.18 |
| Al | 1,350 mg kg$^{-1}$ | 0.050 | 0.10 | 0.015 |
| Ca | 1,680 mg kg$^{-1}$ | 0.062 | 0.13 | 0.019 |
| Cu | 52 mg kg$^{-1}$ | 0.0022 | 0.0040 | 0.00060 |
| Fe | 878 mg kg$^{-1}$ | 0.033 | 0.070 | 0.010 |
| Mg | 1,540 mg kg$^{-1}$ | 0.057 | 0.12 | 0.017 |
| Mn | 77 mg kg$^{-1}$ | 0.0029 | 0.0060 | 0.00090 |
| P | 9,120 mg kg$^{-1}$ | 0.34 | 0.70 | 0.10 |
| K | 10,600 mg kg$^{-1}$ | 0.39 | 0.81 | 0.12 |
| Zn | 260 mg kg$^{-1}$ | 0.0097 | 0.020 | 0.0030 |

**Table 4** Estimated elemental contents of coquí feces and urine (±1 SE, *n*=28), the total expected amount of coquí feces and urine (columns 2 and 3 summed), and existing data on throughfall chemistry in this forest in kg ha$^{-1}$ year$^{-1}$ in the Bisley Watersheds, Luquillo Experimental Forest, Puerto Rico. Coquís were modeled using average densities. Throughfall estimates were collected in El Verde, Luquillo Experimental Forest, Puerto Rico (McDowell 1998; Chestnut et al. 2000), except for *DON*, which was calculated using a typical DOC:DON from the literature (Currie et al. 1996). *DOC* dissolved organic carbon, *DON* dissolved organic nitrogen, *NA* not available

| Element | Eliminated as feces (kg ha$^{-1}$ year$^{-1}$) | Excreted as urine (kg ha$^{-1}$ year$^{-1}$) | Sum of eliminated and excreted (kg ha$^{-1}$ year$^{-1}$) | Throughfall estimate for LEF (kg ha$^{-1}$ year$^{-1}$) |
|---|---|---|---|---|
| Total C | 3.04 | NA | 4.03 | 127 |
| DOC | NA | 0.45±0.10 | – | NA |
| Total N | 0.51 | NA | 1.09 | 8.6 |
| DON | NA | 0.54±0.19 | – | 5.1 |
| $NO_3$ | NA | 0.01±0.009 | – | 3.3 |
| $NH_4$ | NA | 0.18±0.04 | – | 0.18 |
| Al | 1.38E–05 | 0.002±0.0007 | 0.002 | NA |
| Ca | 0.0004 | 0.33±0.075 | 0.33 | 22.7 |
| Fe | 9.81E–06 | 0.002±0.0009 | 0.002 | NA |
| Mg | 2.30E–05 | 0.068±0.017 | 0.07 | 13.4 |
| Mn | 2.34E–06 | 0.0015±0.0003 | 0.002 | NA |
| P | 4.77E–05 | 0.102±0.017 | 0.10 | 0.45 |
| K | 1.38E–05 | 0.31±0.04 | 0.31 | 51.6 |
| Zn | 1.77E–06 | Not Detectable | 1.77E–06 | NA |

urine than in the control samples (*df*=27, *P*<0.001). Elemental analyses of urine produced by one coquí per night resulted in the following average amounts: 1.37E–01 mg DOC, 1.72E–01 mg DON, 6.99E–02 mg $NH_4^+$, 2.42E–03 mg $NO_3^-$, 3.67E–04 mg Al, 7.66E–02 mg Ca, 4.94E–04 mg Fe, 1.59E–02 mg Mg, 3.32E–04 mg Mn, 2.52E–02 mg P, and 7.79E–02 mg K. Using the amount of urine produced by coquís per night, average coquí density, and the element content of urine, the amount of each element excreted by coquís was estimated (Table 4).

From April to December in this forest, males produce 3.4 mg feces day$^{-1}$ and females produce 9.1 mg feces day$^{-1}$, and from January to March, males produce 3.1 mg feces day$^{-1}$ and females produce 7.3 mg feces day$^{-1}$ (Woolbright 1985). Assuming a 1:1 sex ratio and the average dry wt of adult feces as 0.006 g, adult coquís produce 7.2 kg feces ha$^{-1}$ year$^{-1}$. Assuming feces are proportional to biomass, juvenile coquís feces weigh 0.0002 g. Juveniles then contribute 1.2 kg feces ha$^{-1}$ year$^{-1}$ for a total coquí contribution of 8.9 kg feces ha$^{-1}$ year$^{-1}$. Fecal material contained 34.2% C and 5.7% N, and the elemental analyses resulted in the following average concentrations: 1.6 mg kg$^{-1}$ Al, 40.2 mg kg$^{-1}$ Ca, 0.05 mg kg$^{-1}$ Cu, 1.1 mg kg$^{-1}$ Fe, 2.3 mg kg$^{-1}$ Mg, 0.3 mg kg$^{-1}$ Mn, 5.4 mg kg$^{-1}$ P, 1.6 mg kg$^{-1}$ K, and 0.2 mg kg$^{-1}$ Zn. Using the estimated total feces contribution ha$^{-1}$ year$^{-1}$and the element content of fecal material, the amount of each element that coquís eliminate was estimated (Table 4).

A model of nutrient flow in coquí populations in the LEF was constructed using average adult densities of 3,265 individuals $ha^{-1}$, average pre-adult densities of 17,305 individuals $ha^{-1}$, and a total dry wt of 3.3 kg $ha^{-1}$ (Fig. 1; Stewart and Woolbright 1996). Values for ingestion and egestion were from Table 3 and Table 4, respectively. The amount of C respired was calculated using an estimate of the proportion of assimilation energy used as respiration from Stewart and Woolbright (1996). The amount of C and other nutrients remaining were estimated as production. Using a steady-state growth model assumption, production and mortality were set equal.

## Discussion

In this study, coquís were found to increase the pool of essential available nutrients that are known to limit microbial and plant growth in the study forest (Silver et al. 1994). Coquí presence during a 4 month experiment resulted in higher concentrations of most nutrients (including C, N, Ca, P, and K) in leaf wash solutions coming off of forest understory plants and higher concentrations of N, P and K in decomposing leaf litter material on the forest floor. These same nutrients, in particular DOC, $NH_4^+$, Ca, P, and K, were also detected in high concentrations in coquí urine and fecal material, and carcasses. Nutrients, such as $NO_3^-$, Al and Zn, which are in low concentrations in coquí urine and fecal material, and carcasses, were also in low concentrations in leaf wash solutions (Table 1). The results suggest that coquí waste production and population turnover increase the cycling rate of nutrients in the system compared to a system with no coquís. In a related study using the same enclosures, the enclosures with no coquís were shown to have higher arthropod biomass (Beard et al., in review). Therefore, coquís increased nutrient cycling rates in the experimental units over any increase in nutrient cycling rates that may have resulted from the increase in arthropod biomass in the absence of coquís.

Increased nutrient cycling rates occurs when coquís are present because, although their biomass appears small when compared to other pools in the ecosystem, animals return a substantial portion of the nutrients they consume back to the detrital system in the form of concentrated, highly labile liquid and solid wastes, and carcasses (Ruess and McNaughton 1987). In addition, species in higher trophic levels can contribute more to nutrient availability than their prey because their waste and bodies can be more decomposable. For example, amphibian nitrogenous waste is usually in the form of urea (46% N), and invertebrate waste is typically in the form of uric acid, or one of its breakdown products, which is the least soluble form of nitrogenous waste (30% N). Similarly, amphibian bodies lack a hard exoskeleton and are more likely to decompose than are invertebrates; invertebrate bodies can serve as nutrient sinks (Seastedt and Tate 1981). Future studies to test the hypotheses that coquí waste products and carcasses decomposer faster than invertebrate bodies and frass would enhance this research.

The idea that faunal species increase productivity by 'accelerating' the path of nutrients to the available pools and avoiding storage in detritus is not new (Webb 1977). It has long been suggested that faunal species can retain nutrient molecules in the available pool for longer periods of time than they would exist otherwise (Rigler 1973). However, experimental tests of this idea, especially with higher trophic level species in terrestrial systems, have been less explored, most likely because of the difficulties involved in conducting such a test. Our findings suggest that vertebrate predators can play important roles in ecosystem processes by contributing waste material and carcasses and that, in fact, they may even have a greater influence through these mechanisms than herbivores and decomposers. If we assume that vertebrate predators only have effects at the ecosystem level through changes in their prey populations, unexpected ecosystem consequences may result from predator losses.

### Throughfall

Ecosystem studies have documented how throughfall inputs of nutrients can be important in some ecosystems even though concentration levels are typically low compared to other nutrient fluxes within that system (McDowell 1998). In previous studies, for example during herbivorous insect outbreaks, herbivores have been found to contribute significant amounts of nutrients to the soil surface as a result of increasing frass (Lovett and Ruesink 1995) and chemical leaching of foliar surfaces (Tukey and Morgan 1963). Herbivores through these mechanisms have been found to measurably increase nutrient output from an ecosystem (Swank et al. 1981). However, the importance of predators in contributing to internal nutrient fluxes at the ecosystem level in forests and especially as part of processes occurring in forest canopies (e.g., throughfall) has only been examined in a few cases (e.g., Gilmore et al. 1984).

Because of the difficulty involved in detecting the impact of a species on throughfall chemistry with the tremendous spatial and temporal variability that exists at the ecosystem level (McDowell 1998), we used a small-scale experiment to determine whether coquís affect the nutrient concentrations of throughfall (i.e., leaf washes). As predicted, most elements (especially DOC, $NH_4^+$, and K) were detected at higher levels in leaf washes when coquís were present than when they had been experimentally removed (Table 1). While this is not the standard approach for measuring throughfall in these forests (e.g., because water from the canopy was not sampled, McDowell 1998), these numbers illustrate how their local extinction could reduce nutrients in throughfall by 60–100%, if precipitation was of short duration and coquí densities were high. To illustrate how coquís may influence throughfall chemistry at the whole ecosystem level, in Table 4 coquí inputs from urine and feces were modeled at average densities (20,000 individuals $ha^{-1}$). This table shows that, even at average densities, coquís have measurable effects on the input in the system, especially for N and P.

The plant species used in this experiment showed variable responses to coquí presence. *Piper* plants were more efficient at acquiring most surface deposited nutrients (Table 1). However, coquís were only observed sitting on *Piper* leaves during the study; *Piper* leaves were better able to physically support them. Coquí effects on *Manilkara* leaf wash chemistry were due to coquí-associated atmospheric deposition, suggesting that coquís do not need to sit on leaves to affect the amount of nutrients coming off the foliage. A different plant response to coquís has implications for other ecosystem responses. For example, early successional species, which are more likely to respond to nutrient pulses, should respond more quickly to coquís (Fletcher et al. 1996). Coquís may increase the rate of forest succession following disturbances when early successional plant and coquí densities are high.

One difficulty in using small scales to measure effects of a species on plants is that plant species composition included in the experimental system will determine what kind of responses are measurable. In this study, understory plants were used to determine the effect of coquís on throughfall and foliar chemistry. Even though invertebrate densities are greater closer to the forest floor (Garrison and Willig 1996), coquís do not often forage on litter invertebrates (Beard et al., in review). Coquís forage more heavily in the canopy where competition for insects is great, and coquí effects on reducing their prey is expected to be greater in the canopy than the understory (Dial and Roughgarden 1995; Stewart and Woolbright 1996). However, we expect that coquí effects on increasing available nutrients on the forest floor through waste material and carcasses will not depend on their vertical location while foraging. Despite this, understory and canopy plants could have different responses to coquís and caution should be used when scaling responses from understory to canopy plants.

## Leaf litter

Leaf litter decomposition and mineralization rates have long been considered important variables to the potential production on a site (Anderson and Swift 1983). Many studies have been conducted to determine the importance of waste production and population turnover of decomposer organisms in controlling litter decomposition rates (Coleman et al. 1978; Ineson et al. 1982); however, few have studied the importance of predator waste production and turnover (Hanlon 1980). In a related study on leaf litter decomposition using the same enclosures, after 4 months 55.4 ± 6% (mean ± SE) of the original leaf biomass remained in enclosures with coquís and 69.1 ± 5% of the original leaf biomass remained in enclosures without coquís (Beard et al., in review). The observed changes in C:N ratios in the leaf litter with and without coquís from the present study support the finding that coquís increased decomposition rates (Melillo et al. 1982). The results suggest that increased nutrient availability associated with coquís caused this change. It is not clear whether decomposition rates increased as a result of coquí waste products or carcasses (ten carcasses in total). It would be important in future studies to separate these mechanisms.

During this study, coquí exclusion from the system lead to a 12.1% and 13.5% decrease in the amount of the K and P, respectively, available to organisms decomposing leaf litter (Table 2). If these results were scaled to the ecosystem level, using an average forest floor litter weight of 6,000 kg ha$^{-1}$ (Weaver and Murphy 1990), coquí removal from the system would decrease the amount of K available for decomposing the forest litter from 6.6 to 5.7 kg ha$^{-1}$ and the amount of P available from 3.7 to 3.1 kg ha$^{-1}$. The decrease in both K and P concentrations in the absence of coquís has implications for nutrient cycling rates since both elements are considered to limit microbial activity and plant growth in this forest (Silver et al. 1994). Also, since pulsed nutrient inputs can maintain ecosystem functioning in the wet tropics (Lodge et al. 1994), faunal species may contribute significantly to this mechanism.

## Coquís and invertebrates

To validate our findings, we compared our model of nutrient fluxes in and through coquí populations to a similar model created for a salamander, *Plethodon cinereus*, in the Hubbard Brook Experimental Forest, New Hampshire (Burton and Likens 1975a, b). We found that nutrient concentrations were an order of magnitude higher in coquís than in the salamanders even though elemental concentrations were similar (Table 5). This was expected since the standing stock of coquís is approxi-

**Table 5** Comparison between the average nutrient concentrations (in %) and average standing stock of nutrients (in g ha$^{-1}$) of *Plethodon cinereus* populations in the Hubbard Brook Experimental Forest, New Hampshire (Burton and Likens 1975a, b) and *Eleutherodactylus coqui* populations in the Luquillo Experimental Forest, Puerto Rico

| Element | Standing stock of salamanders | | Standing stock of coquís | |
|---|---|---|---|---|
| | (%) | (g ha$^{-1}$) | (%) | (g ha$^{-1}$) |
| C | 43.84 | 171 | 43.92 | 1,440 |
| N | 9.06 | 37.44 | 11.88 | 390 |
| Ca | 3.43 | 11.86 | 3.54 | 116.17 |
| Mg | 0.13 | 0.54 | 0.14 | 4.50 |
| P | 2.28 | 7.26 | 2.53 | 75.49 |
| K | 0.87 | 3.11 | 1.02 | 33.42 |
| Zn | 0.011 | 0.03 | 0.0082 | 0.27 |

mately 10 times higher than that of salamanders; *P. cinereus* has an average density of 2,600 individuals ha$^{-1}$ (Burton and Likens 1975a). While the quantity of nutrients available from *P. cinereus* waste and production may be lower than that from coquís, it would be interesting to determine which species provides more available nutrients to the plant and decomposers in its respective ecosystem.

Based on the difference between the estimated amount of the total nutrients eliminated and excreted (Table 3) and the amount egested by coquís (Table 4), coquís positively assimilate metal ions such as Al, Cu, Fe, and Zn and negatively assimilate Ca, Mg, Mn, and K. This was expected since there are no mechanisms for faunal species to eliminate metal ions from tissues. The high percentage of P in both *P. cinereus* and the coquí indicates that both species are sinks for the element (Burton and Likens 1975b). Decomposing coquí bodies could be an important source of this nutrient since it is limiting in this system. The diagram in Fig. 1 shows more Ca being egested than ingested. This may have occurred because the estimate for ingested nutrients did not include snails, which are important prey items and high sources of calcium.

## Implications

Disturbances, such as hurricanes and treefalls, are driving variables in the structure and functioning of the Luquillo Experimental Forest, Puerto Rico (Foster et al. 1997). The results from this study suggest that the coquí, because it increases nutrient availability at the ecosystem level and because its density increases following hurricane and treefall events, may play an important role in ecosystem resilience and recovery. Following a disturbance, the ability of plants to obtain adequate nutrients is critical to reestablish production levels. This is especially true because litter inputs dramatically decline and there is very little canopy for throughfall-leaching (Scatena et al. 1993). Following disturbances, the increase in coquí input on plants and the increase in the number of decomposable frog carcasses may become major pathways of nutrient input.

The type, frequency, and severity of the forest disturbance will alter the effect of the coquí both temporally and spatially. Hurricane Georges was not as severe as Hurricane Hugo, and, likewise, after Georges the coquí population increase was smaller and shorter-lived (L.L. Woolbright, unpublished data; Woolbright 1996). Adult numbers roughly doubled following Georges, whereas they increased six-fold following Hugo. Their increase after treefall events similarly depends on the severity of the disturbance (i.e., the amount of habitat structure added to the forest floor). Furthermore, coquí effects following hurricanes are more spatially homogeneous at the landscape level than those following treefall events. However, in both situations, the increase in coquí density may be viewed as a type of "outbreak". Since the experiment in this study was conducted using post-disturbance densities, it would be interesting in future studies to look more specifically at how shifting coquí densities influence their role in the ecosystem.

Even when not considering disturbance events, the species-specific effects found in this study will vary temporally and spatially in the study forest. Even though adult abundance is constant throughout the year, adults forage and defecate more and juvenile abundance is greater during the rainy season than during the dry season (Stewart and Woolbright 1996). In addition, since plants are actively taking up nutrients during the rainy season, plants may more efficiently utilize coquí-induced increases in nutrient availability at these times. Therefore, coquí effects may be greater during the rainy months, or in the months this experiment was conducted. As a final point, depending on the scale of investigation, coquí effects across the landscape may appear heterogeneous (i.e., greatest near perch sites) or homogeneous considering their high and even population density in the forest (Beard et al., 2002). Experiments that specifically address hypotheses about how coquí impacts depend on seasonality and the temporal and spatial scale of investigation would enhance our understanding of their effects in the study forest.

Studying the role of coquís in ecosystem processes provides some understanding for how coquís, and similar species, may affect systems where they are declining or have been introduced. Unlike other *Eleutherodactylus* spp. in Puerto Rico, which have more specific habitat requirements, such as the cave-dwelling *E. cooki*, the coquí has not experienced great population declines. No clear understanding of what is causing the declines in other *Eleutherodactylus* species has been reached (Stallard 2001). In addition, the global distribution of the coquí has been expanding in recent years. The coquí has been introduced into at least four locations outside of Puerto Rico, and most recently Hawaii, U.S. (Kraus et al. 1999). The present research suggests that nutrient cycling rates will decrease where *Eleutherodacytlus* spp. are lost and that nutrient cycling rates will increase where coquís invade. Studies of nutrient cycling rate changes where coquís are invading would greatly add to our understanding of the role of native and non-native vertebrate species in influencing ecosystem functions.

A recent review of the literature on the role of insect carcasses and frass has shown that different impacts on ecosystem processes are found depending on the system (Hunter 2001b). Like insects, the magnitude of the influence of predators on changes in ecosystem level nutrient influxes, and their subsequent effects on nutrient cycling rates will likely depend on the system under study (Schowalter 1999). However, a few general hypotheses emerge from our results. Predators that are highly abundant and not replaced functionally when removed are more likely to be important in nutrient cycling. Animal waste products and carcasses can become homogeneous nutrient sources if population densities are sufficiently high; otherwise, their effects may be important nutrient pulses. The nutrients made available by species and those limiting to the system will dictate which species are important to nutrient dynamics. Our study system is unique because of its high amphibian densities and lower overall diversity compared with continental areas. Future studies should be designed to determine whether our findings are unique or whether other vertebrate predators affect terrestrial nutrient cycling rates through the addition of available nutrients in their waste material and carcasses.

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