Journal of Tropical Ecology (2007) **23**:161–168. Copyright © 2007 Cambridge University Press
doi:10.1017/S0266467406003932 Printed in the United Kingdom

Toads (*Bufo bankorensis*) influence litter chemistry but not litter invertebrates and litter decomposition rates in a subtropical forest of Taiwan

Ching-Yu Huang*, Chiao-Ping Wang† and Ping-Chun Lucy Hou*[1]

* Department of Life Sciences, National Cheng Kung University, Tainan 701, Taiwan
† Fushan Research Center, Taiwan Forestry Research Institute, I-lan 260, Taiwan
(*Accepted 21 November 2006*)

Abstract: Few studies have been conducted to investigate ecological roles of litter amphibians in forest ecosystems. In this study, ten field enclosures (3 m × 2 m × 0.4 m) were used to evaluate effects of the toad *Bufo bankorensis* on the abundance of litter invertebrates (microbivores, fragmenters and predatory arthropods) and litter decomposition rates in a subtropical forest of southern Taiwan. Litterbags collected from toad and control (toad-excluded) enclosures were analysed for the communities and abundances of litter invertebrates and decay loss during this decomposition study from September to December 2001. The presence of *B. bankorensis* significantly changed phosphorus concentrations in the litter, but not the densities of litter invertebrates (microbivores, fragmenters and predatory arthropods) or rates of litter decomposition. These results were not consistent with previous studies, which have shown that *Plethodon cenereus* in a temperate forest of north-east USA and *Eleutherodactylus coqui* in a tropical rain forest of Puerto Rico significantly changed decomposition rates. We suggest that ecological roles of ground-dwelling amphibians may be species-specific and vary with different terrestrial ecosystems.

Key Words: amphibian, fragmenters, lowland rain forest, microbivores, Nanjenshan, nutrient cycling, predators, top-down control

INTRODUCTION

Litter decomposition is an important process for biogeochemical cycles and plant production in terrestrial ecosystems. Previous studies have shown that litter quality and quantity, climate and litter fauna play significant roles in litter decomposition processes (Aerts 1997, Couteaux *et al.* 1995, Wardle & Lavelle 1997). Because temperature and moisture fluctuations are minor in the tropics, litter invertebrates are hypothesized to play a more significant role in litter decomposition in tropical forests (González & Seastedt 2000, Hou *et al.* 2005). Litter invertebrates can be roughly divided into three functional groups by feeding guild: microbivores, fragmenters and predators (Coleman *et al.* 2004). The microbivores, mainly mites (i.e. oribatids) and collembolans, affect litter decomposition by grazing on bacteria and fungi (Coleman *et al.* 2004). In contrast, the fragmenter group (such as earthworms and millipedes) not only directly consume leaf litter, but also indirectly facilitate the utilization of leaf litter by micro-organisms by increasing contact surface areas of litter (Edwards & Bohlen 1996, Wolters & Ekschmitt 1977). The predatory arthropods (i.e. spiders and ants) may exert top-down control on the litter decomposition in detrital food webs by regulating their prey populations (microbivores and fragmenters) (Kajak & Jakubczyk 1977, Wise 2004). Thus, litter invertebrates may have differential ecological impacts on detrital food webs based on their population dynamics and their interactions with other functional groups.

In contrast to many studies concerning the importance of litter invertebrates in detrital food webs, few studies have examined the potential influence of vertebrate predators on detrital food webs, particularly their effects on litter invertebrates and litter decomposition. In tropical forests, amphibians are the major vertebrate predators inhabiting litter layers (Caldwell & Vitt 1999). Their diets comprised of various litter invertebrates, including spiders and ants (predators), amphipods and millipedes (fragmenters), and collembolans and mites (microbivores)

---

[1] Corresponding author. Email: pchou@mail.ncku.edu.tw

(Caldwell & Vitt 1999, Lima *et al.* 2000, Simon & Toft 1991, Stewart & Woolbright 1996, Toft 1980). Therefore, amphibian predation likely alters the densities and communities of litter invertebrates, and can indirectly assert a top-down control on the litter decomposition. Even so, the potential impacts on detrital food webs by amphibians may depend on their feeding strategies. Smaller frogs feed mostly on the microbivores, and thereafter may facilitate litter decomposition as they reduce the grazing and predatory intensity of the mites and collembolans on bacteria and fungal populations. Interestingly, opposite results on litter decomposition may occur if amphibians exert greater influence on predatory invertebrates than on microbivores, thereby releasing the microbivores from predation pressure. Feeding preferences of amphibians may dictate consequences on ecosystem function in terrestrial ecosystems.

Recently, several studies have investigated the ecological roles of ground-dwelling amphibians in forest ecosystems (Beard *et al.* 2002, 2003; Rooney *et al.* 2000, Wyman 1998). Wyman (1998) showed that red-backed salamanders (*Plethodon cinereus*) consumed significant numbers of litter fragmenters (e.g. larvae of Coleoptera and Diptera), and indirectly reduced rates of decomposition by 11–17%, in a temperate forest of the eastern United States. Rooney *et al.* (2000) found the same species of salamander to increase collembolan abundance by consuming predators of the collembolans such as the ants. Studies by Beard *et al.* (2002, 2003), however, suggested that amphibians affect litter decomposition in a different way. They discovered that the coqui frog (*Eleutherodactylus coqui*) in Puerto Rico had significant effects on litter decomposition rates and nutrient cycling via its waste products and population turnover rather than by the trophic relationships with litter invertebrates in a tropical forest ecosystem. Based on these studies, litter amphibians of different terrestrial ecosystems can affect litter decomposition and nutrient cycling in various ways, either through their own population dynamics or trophic effects with litter invertebrates. As declines in amphibian populations on a global scale are becoming increasingly well documented (Houlahan *et al.* 2000, Lips 1998), there is an urgent necessity to understand and determine their ecological roles in different terrestrial ecosystems.

The purpose of this study is to quantify the ecological importance of a litter amphibian by evaluating its impacts on invertebrate communities and litter chemistry and decomposition rates in a subtropical forest of Taiwan. Our hypotheses are that litter amphibians will (1) reduce the abundance of litter invertebrates (microbivores, fragmenters and predators) and change the community composition of litter invertebrates, and (2) indirectly affect the litter chemistry and rates of litter decomposition.

METHODS

Study area

This experiment was conducted at the Nanjenshan Nature Reserve (22°03′N, 120°51′E) of southern Taiwan, which is one of Taiwan's Long Term Ecological Research (LTER) sites. The elevation ranges from 300 to 500 m asl. Annual mean temperature is 22.3 °C, and annual precipitation is 3500 mm. About 230 rainy days are evenly distributed throughout the year in this area. However, heavy rainfall resulting from tropical typhoons usually occurs from July to September. The north-easterly monsoon winds blow continuously to this area from October to late February each year, and have chronic and cumulative effects on forest structure and composition (Sun *et al.* 1998).

Vegetation in this area is varied and dependent on topography and the influence of monsoon winds. On the exposed slope, vegetation is dominant by the shrub, *Eurya hayatai* Yamamoto, while the tree species, *Castanopsis carlesii* (Hemsl.) Hayata and *Illicium arborescens* Hayata, are dominant on the gentle leeward slope. The most dominant species by the streamside is *Schefflera octophylla* (Lour.) Harms. Annual litterfall was estimated at 10.8 and 8.5 Mg ha^{-1} for 1995 and 1996, respectively. Two peaks of litterfall occur at the beginning of the growing season (March–May) and the typhoon season (July–September). Soils are acidic Ultisols ($pH_{water} < 5.0$) of typical mull humus type. Soil description in this area can be found in Chen *et al.* (1998) and Tsui *et al.* (2004).

Experimental design

Ten enclosures were set up in a wind-shielded creek area within a 2-ha permanent plot near Nanjen Lake in the Reserve. Each enclosure was 3 m × 2 m and 35–40 cm tall. One aluminium post was fixed at each corner (10 cm deep) to support the enclosures. Top and sides of the enclosures were covered with 0.1-mm mesh screen to prevent migration of litter invertebrates and toads. No vertebrate predators were found in the enclosures before the experiment started. Five enclosures were randomly selected as the toad group with introduction of one male adult toad (*Bufo bankorensis* Barbour) into each enclosure; while the other half served as control (toad-excluded) group. We chose *B. bankorensis* for this study because of its dominant abundance in this research area (Huang & Hou 2004) and the highest amount of food items in its stomach (17.9 items per stomach) as compared to other forest floor-dwelling amphibians (ranid frogs with 2–3 items per stomach) (Hou unpubl. data). The amphibian density in toad enclosures (0.17 individuals m^{-2}) was within the ranges (0.03–0.18 individuals m^{-2}) observed in a previous field surveys (Huang & Hou 2004). The diet of *B. bankorensis* consists mainly of ants (53%), coleopterans (16%) and termites (9 %) (Hou unpubl. data). Same sizes of toads were chosen for this experiment, and body weight and snout–urostyle length of the toads were measured at the beginning (26.7 ± 0.9 g and 66.3 ± 1.0 mm, respectively) and the end of experiment for monitoring their growth.

Litterbags (20 × 20 cm) with 5-mm mesh size were used for including most of litter invertebrates (microbivores, fragmenters and predators). As *Schefflera octophylla* (Araliaceae) was widely distributed and dominant over the study area, their fresh fallen leaves were collected and air dried during July and August 2001. Approximate 4.5 g of air-dried leaves were placed in each litterbag for evaluating litter decomposition. A subsample of litter was oven-dried and weighed for calibrating the initial dried weights.

We collected all surface litter in 15 × 15 cm of each enclosure at the beginning and the end of the experiment to evaluate the changes of litter invertebrates in the floor. Because the litter amount varied within all samples, the densities of litter invertebrates were represented by per gram dried litter (individuals g^{-1}) rather than by collected area (individuals m^{-2}). Air temperature and humidity were recorded every 8 s for both in the enclosures and in the field during the whole experimental period. Soil pH and moisture were measured at every sampling date in all enclosures as well as nearby soils.

Six litterbags were buried in litter layers in each field enclosure on 12 September 2001 and one litterbag was randomly collected every 14–21 d for determining the invertebrate community and litter decomposition rate. Each collected litterbag was placed in a separate plastic bag for transport to the laboratory.

Litter and fauna analysis

Litter macro-invertebrates were hand-picked and the rest of the invertebrates in the litterbags (litterbag invertebrates) and litter samples (litter invertebrates) were extracted by a Tullgren-funnel at room temperature. All invertebrates were preserved in 75% ethanol for identification, and classified into broad taxonomic groups such as Acari and Collembola. We classified invertebrates into functional groups by feeding guild: microbivores (mites and collembolans), fragmenters (Amphipoda, Diplopoda, Isopoda and earthworms) and predators (ants, Coleoptera, Insecta larvae, pseudoscorpion, spiders).

After faunal extraction, litter was oven-dried at 75 °C for 48 h for dry weight determination and then finely ground (< 0.5 mm) for nutrient analysis. Following the dry combustion method, 2 mg of ground litter was used for carbon (C) and nitrogen (N) concentration measurement by the CN elemental analyser (EA, Thermo Finnigan NA1500). For potassium (K), sodium (Na), calcium (Ca), magnesium (Mg) and phosphorus (P) analysis, 0.5-g samples were ashed at 490 °C. Ash was dissolved in 5 ml 2N HCl, washed into 50 ml in a flask with distilled deionized water, and filtered (Munson & Nelson 1990). Elements were determined by inductive-coupled plasma (ICP, Jobin-Yvon Horiba group, JY2000, Edison, USA). Litter C, N and main mineral nutrients (K, Na, Ca, Mg and P) were analysed for initial and the last litterbag sampling (day 107) to compare the differences between treatments (toad and toad-excluded).

Statistical analysis

The toad effect on the remaining litter dry mass and the densities of total invertebrates in the litterbags were analysed by repeated-measures procedure using SAS (SAS Institute, Cary, New York, USA). Data of litter invertebrate densities, litter C, N and, mineral nutrients (K, Na, Ca, Mg and P) from the final sampling were analysed using the student t-test for toad treatments. Paired t-test was used to analyse the changes of snout–urostyle length and weight of the toads and the enclosure effects on the environmental data (air temperature and humidity, soil pH and soil moisture) during the experiment. The potential relationships of total litterbag invertebrate densities with main groups of litter invertebrates (mites and collembolans), remaining litter mass, litter nutrients (C, N and mineral elements) and the environmental factor (precipitation) were examined by using Pearson Correlation. We also ran Pearson Correlation for the relationships among different functional groups of litter invertebrates, including microbivores, fragmenters and predators. Invertebrate composition data were fourth-root-transformed before applying non-parametric multivariate analysis of similarity (ANOSIM) in PRIMER program (Clarke & Warwick 1994, PRIMER-Ltd, Roborough, Plymouth, UK.). The ANOSIM procedure basically used permutation/randomization methods on a similarity matrix to calculate similarities of the invertebrate communities among treatment and time factors. We conducted two-way crossed ANOSIM based on Bray & Curtis similarity values calculated from transformed density data for testing the differences of invertebrate communities between toad treatments and among sampling times.

RESULTS

Enclosure effects

The toads significantly reduced their body weights from average 26.4 to 22.3 g at the end of experiment (t = 4.8,

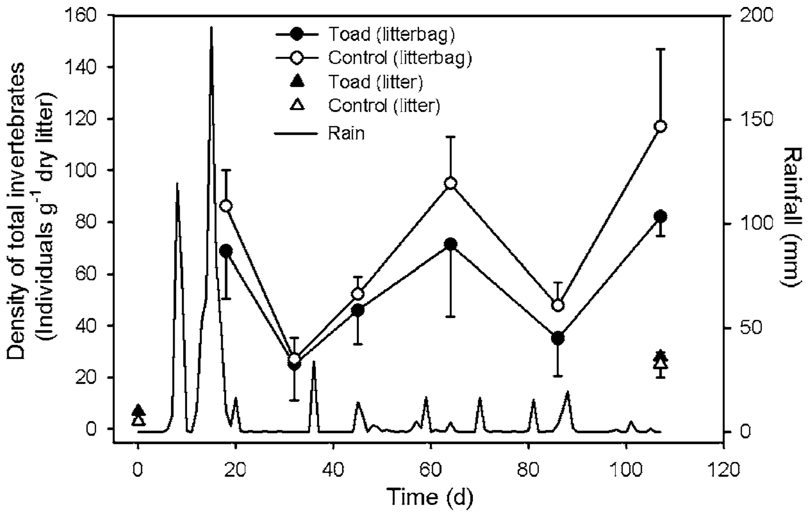

Figure 1. Density of total litter invertebrates from the toad, *Bufo bankorensis* (filled symbols) and control (open symbol) enclosures in Nanjenshan forest, Taiwan. Circle and triangle symbols represent the mean values (± 1 SE) of litterbags and litter samples, respectively. Rainfall during the experimental period is shown by solid line.

$P < 0.01$). The snout–urostyle length of the toads did not change during the experimental period ($t = 0.9$, $P = 0.4$).

The field enclosure method changed air temperature and humidity, but the effects are minor. The enclosures raised air temperature and relative humidity by only 0.03 °C and 1.52%, respectively. The enclosures had no significant influence on soil pH and soil moisture ($P > 0.1$; data not shown) during the experimental period. We found that the perturbation from setting up the enclosures reduced total abundance of litter invertebrates in the enclosures as compared with that in the forest floor (Density: mean ± 1 SE = 5.0 ± 1.2 and 11.8 ± 2.4 individuals g^{-1} dry litter, respectively; $t = -2.55$, $P = 0.02$) at the beginning of the experiment. However, litter invertebrate population recovered during the experimental period, and the density increased to 2.5–5 times higher at the end of experiment (Figure 1). There was no significant difference in litter invertebrate communities (ANOSIM, $R = 0.52$, $P = 0.25$, Table 1) and densities ($t = -0.81$, $P = 0.15$, Table 1) between toad and control enclosures at the end of experiment.

Table 1. Mean density of invertebrates collected from litterbags and litter samples within the enclosures at the end of experiment (day 107) in Nanjenshan forest, Taiwan. Densities are measured by number of individuals per gram dried litter and are shown as mean ± 1 SE.

	Litter		Litterbag	
Invertebrate group	Toad	Control	Toad	Control
Microbivore				
Acarina	15.2 ± 5.09	16.1 ± 3.70	39.8 ± 8.70	54.8 ± 13.6
Collembola	8.62 ± 0.62	4.63 ± 0.93	36.3 ± 1.60	54.0 ± 16.0
Total microbivores	23.9 ± 6.81	20.8 ± 4.39	76.0 ± 7.16	109 ± 28.8
Fragmenter				
Amphipoda	0.13 ± 0.06	0.04[a]	0.59[a]	0.78[a]
Isopoda	0.32 ± 0.09	0.05 ± 0.03	1.02 ± 0.6	3.11 ± 1.40
Diplopoda	0.10[a]	0.10 ± 0.08	0.67[a]	0.25 ± 0.16
Oligochaeta	0.03 ± 0.02	0.1[a]	1.0[a]	0.32 ± 0.19
Total fragmenters	0.89 ± 0.24	0.89 ± 0.60	1.95 ± 0.90	4.88 ± 1.70
Predator				
Araneae	0.36 ± 0.16	0.40 ± 0.17	1.05 ± 0.55	1.37 ± 0.28
Coleoptera	0.38 ± 0.12	0.17 ± 0.07	0.31 ± 0.18	2.39[a]
Formicidae	1.47 ± 1.36	0.46 ± 0.39	0	0
Pseudoscorpionidae	0.20 ± 0.07	0.16 ± 0.08	1.3 ± 0.61	0.38 ± 0.23
Insecta larvae	0.39 ± 0.19	0.71 ± 0.54	0.37 ± 0.13	1.05 ± 0.41
Total predators	2.41 ± 0.49	1.19 ± 0.41	2.66 ± 0.76	2.32 ± 0.71
Total invertebrates	27.9 ± 7.94	25.2 ± 4.64	81.9 ± 7.19	116 ± 30.2

[a] Value represents only one datum.

Litterbag and litter invertebrate communities

Densities of total litterbag invertebrates did not differ significantly between the toad and control enclosures ($F_{1,7} = 2.1$, $P = 0.19$) and there was no interaction between treatments and time ($F_{5,35} = 0.5$, $P = 0.6$). However, an oscillation over time was observed in this experiment ($F_{5,35} = 10.5$, $P = 0.0012$; Figure 1). This fluctuation of total litterbag invertebrates was only correlated with the densities of mites ($r = 0.92$, $P < 0.01$) and collembolans ($r = 0.94$, $P < 0.01$) in the litterbags, but not related to precipitation, remaining litter mass, or any litter nutrient contents (i.e. C, N and other elements) (all tests $P > 0.1$). However, we found that the abundance of the microbivores was positively correlated with that of the fragmenters ($n = 59$, $r = 0.50$, $P < 0.001$), but not associated with the predators ($n = 59$, $r = 0.13$, $P = 0.32$). The communities of litterbag invertebrates categorized by taxonomic and functional groups both significantly changed with sampling time (ANOSIM, $R = 0.38$, $P = 0.001$; $R = 0.25$, $P = 0.001$, respectively), but not affected by the treatment (i.e. toad presence) ($R = -0.03$, $P = 0.65$; $R = 0.04$, $P = 0.21$, respectively).

Litter decomposition and nutrients

Decomposition of *Schefflera octophylla* litter in this study followed a universal pattern. Litter biomass began with a rapid loss through leaching, then followed a slower decomposition ($F_{5,40} = 24.3$, $P < 0.0001$; Figure 2). The presence of *B. bankorensis* did not have any significant effects on the decomposition rate ($F_{1,8} = 0.38$, $P = 0.56$; Figure 2), and there was no interaction between treatment and time factors ($F_{5,40} = 1.18$, $P = 0.33$; Figure 2).

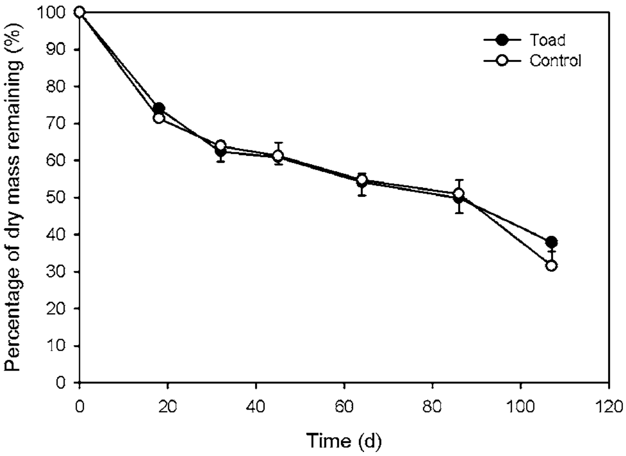

Figure 2 The effects of *Bufo bankorensis* on the remaining percentage of dry mass in *Schefflera octophylla* leaves from the litterbags in Nanjenshan forest, Taiwan. Filled and open symbols represent mean values (± 1 SE) for the toad and control enclosures, respectively.

Table 2. Nutrient analysis of *Schefflera octophylla* of the litterbags in control and toad enclosures at the end of experiment in Nanjenshan forest, Taiwan. Data are shown as mean ± 1 SE.

	Schefflera octophylla litter		
		Final (day 107)	
	Initial (day 0)	Toad	Control
C %	55.0	58.5 ± 0.6	57.9 ± 0.4
N %	1.62	2.28 ± 0.07	2.46 ± 0.10
C/N	33.8	25.8 ± 0.8	23.8 ± 1.1
Ca (mg g^{-1})	12.6 ± 0.14	10.1 ± 2.5	12.3 ± 1.0
K (mg g^{-1})	16.9 ± 0.41	0.89 ± 0.18	0.72 ± 0.07
Mg (mg g^{-1})	5.97 ± 0.10	3.11 ± 0.45	3.15 ± 0.09
Na (mg g^{-1})	1.15 ± 0.02	0.42 ± 0.06	0.40 ± 0.02
P (mg g^{-1})	4.08 ± 0.08	6.25 ± 0.13	5.69 ± 0.10*

*represents statistically significant difference between treatment groups by using t-test ($\alpha = 0.05$).

There was also no toad effect on litter C and N concentrations ($t = -0.85$, $P = 0.43$; $t = 1.19$, $P = 0.29$, respectively), and litter K, Na, Ca and Mg (all tests $P > 0.1$; Table 2). However, we found that litter phosphorus concentration in the toad enclosures (6.25 mg g^{-1}) was significantly higher than that in the control ones (5.69 mg g^{-1}) ($t = -3.3$, $P = 0.01$; Table 2).

DISCUSSION

Litter decomposition is strongly related to total abundance and communities of litter invertebrates, and there is a positive correlation between litter decomposition (annual decay rates, *k*) and the abundance of litter fauna (González & Seastedt 2001, Hou *et al.* 2005, Reddy & Venkataiah 1989). Ground-dwelling amphibians can have a top-down control on litter decomposition because of their trophic effects cascading in detrital food web. Red-backed salamanders (*Plethodon cinereus*), which mainly consume soil and litter invertebrates, cascaded their predatory pressure on key leaf-litter fragmenters to decomposition rates in a temperate deciduous forests of eastern United States (Wyman 1998). In our study, *Bufo bankorensis* had no significant effects on either predatory arthropods (spiders and ants), which mainly constituted its diet, or the fragmenters and the microbivores. Predation pressure by the toads may not be strong enough to cause the changes on their prey populations (microbivores, predators and fragmenters) in this study. However, we did observe a positive correlation between microbivores and fragmenters. The comminution and excretion by the fragmenters may result in the succession of microbial communities (bacteria and fungi) and sequentially affect the population dynamic of the mites and collembolans.

On the other hand, forest-floor amphibians can also affect the litter decomposition process through their own population dynamics. The Puerto Rican frog, *Eleutherodactylus coqui*, enhanced nutrient cycling of the forest ecosystem via its waste production and population turnover rather than the trophic relationships with litter invertebrates in the Luquillo Experimental Forest of Puerto Rico (Beard *et al.* 2002, 2003). The diet of *E. coqui* included all level of litter invertebrates and aerial/canopy arthropods (roaches and crickets) (Stewart & Woolbright 1996). Beard *et al.* (2002, 2003) found higher potassium (K) and phosphorus (P) concentrations in leaf litter and faster decomposition rates, but little change in the abundance of litter invertebrates, with the presence of *E. coqui* frogs in the small-scale ($1\,m^3$) enclosures. They also found that K and P concentrations were high within the invertebrate population (Table 3 in Beard *et al.* 2002). *Eleutherodactylus coqui* converted their prey (i.e. the insects) into nutrient forms in the urine and faecal material which are readily available for the microbes and plants to use. They concluded that this mechanism facilitated the decomposition rates rather than their predation on litter invertebrates. The toad, *B. bankorensis*, did change P concentration in the litter, but had no effects on other elements/nutrients and litter decomposition. It is difficult to clearly elucidate that this P change by *B. bankorensis* was from its egestion or microbial immobilization, because we did not collect toad urine or faecal samples nor measure microbial populations and activities in this study. However, this increment of P availability in the 107-day decomposed litter by *B. bankorensis* could provide as high as 4.76 kg ha^{-1} phosphorus ($+0.56\,mg\,P\,g^{-1}$ litter × $8.5\,Mg\,ha^{-1}$ litterfall in 1996) annually to the forest soils. This supply of phosphorus can play an important role on microbial activities, nutrient cycling, primary production and further relationships between soil properties and vegetations in the forest ecosystem, especially tropical forests (Tsui *et al.* 2004, Vitousek & Sanford 1986). More efforts are needed to investigate the mechanism of this P pulse input by amphibians and potential influences on the litter decomposition process and nutrient cycling in long-term studies.

Amphibian impacts on litter decomposition processes varied in different terrestrial ecosystems. *Plethodon cinereus* slowed down the litter decomposition by decreasing invertebrate abundance in the temperate deciduous forests of the eastern United States, while *E. coqui* enhanced the decomposition by waste production in the tropical forest of Puerto Rico (Beard *et al.* 2002, 2003; Wyman 1998). *Bufo bankorensis* showed no influence on litter decomposition in the subtropical wet forest of Taiwan, Asia. These inconsistent findings indicated that ecological roles of amphibians are not parallel in all terrestrial ecosystems.

This apparent discrepancy of amphibian impacts on litter decomposition in different terrestrial ecosystems may be partly explained by different body sizes and feeding preferences of amphibians. The characteristics of relatively smaller body size and usage of habitat (i.e. tree dwelling) may elucidate how *E. coqui* affected the ecosystem functions through herbivore populations and nutrient release pathways rather than the regulation on litter fauna as compared with the other two species which inhabited the forest floor (the toad: *B. bankorensis* and the salamander: *P. cinereus*).

The abundance of frog communities in the forest ecosystems may also contribute to these inconsistent consequences. There is a general pattern showing that the densities of litter herpetofauna (amphibians and lizards) in Asian forests were lower than those of Neotropical forests (Huang & Hou 2004). The densities of *P. cinereus* in the Huyck Preserve (New York State) and *E. coqui* in Luquillo Experimental Forest (Puerto Rico), which were 50 and 114 individuals per $100\,m^2$, respectively, were both higher than that of total amphibians (10.2 individuals per $100\,m^2$) in Nanjenshan forest of this experiment (Beard *et al.* 2002, Huang & Hou 2004, Wyman 1998). The amphibian densities in the Nanjenshan forest might be too low to cascade their effects on litter invertebrates to detritus biomass. The significance of the potential influences of the amphibians on the ecosystem function may vary with the abundance of amphibian species in different forest ecosystems.

Another explanation of the differing results may come from issues of experimental scale. Beard *et al.* (2003) conducted field experiments on two scales (1-m^3 enclosures and 20 × 20-m exclosures) to evaluate the potential effects of *E. coqui* in the forest ecosystems. Most of the variables (i.e. herbivore abundances and foliage productions) at both scales showed the same patterns and directions; however, they observed more significant differences in the small-scale enclosures. The highlighted effect in the small-scale experiment might be caused by the constraint of the predation and excretion of *E. coqui* within the extremely small enclosures. In our study, the size of enclosures ($2.4\,m^3$) was within the range of the small and large scales used by Beard *et al.* (2003). But our field enclosures did not enhance the toad effects in the condition with their low density. The limited number of replicates (enclosures, $n = 5$) in this study did decrease the power of statistical analysis to detect the toad effects, and the power value of retrospective power analysis for toad effects on invertebrates was 0.69. These data should be explained with caution. On the other hand, the toads are usually considered to be active foragers (Taigen & Pough 1983, Toft 1980) in contrast to *E. coqui* being sit-and-wait (ambush) predators (Stewart & Woolbright 1996). Mean distance travelled per night by *B. bankorensis* is 14.7 m and its home range is $171.1\,m^2$ (minimum convex polygon, MCP, method; Wei & Hou, unpubl. data), which was wider than mean activity radius and home range areas of *P. cinereus* ($3.85\,m^2$, MCP method) (Kleeberger & Werner 1982). If 3 × 2 × 0.4-m enclosures did limit the toad's foraging areas, then higher predation pressure in the toad enclosures should cause significant reduction on the abundance of litter invertebrates. However, this was not observed in the experiment. We suggest that *B. bankorensis* may affect forest ecosystem functions via nutrient cycling (such as phosphorus) in various ways, instead of by direct regulation of their prey populations.

Amphibians can play different roles in diverse terrestrial ecosystems. Their natural history, including feeding strategies, habitat usages and population abundances, can affect their importance and their ecological roles in the ecosystems. They may regulate litter decomposition and plant production by controlling the populations of litter invertebrates on the forest floor and herbivore populations above ground. Hence, we suggest that amphibian impacts on ecosystem function may be mainly species- and ecosystem-determined. More research is necessary to clarify the importance of amphibians in various types of terrestrial ecosystems.

ACKNOWLEDGEMENTS

We thank the students from the Tadpole Laboratory for field sampling assistance, the two anonymous reviewers for valuable comments on the earlier version of the manuscript and J. Welch and S. Connelly for reviewing the manuscript. This study was supported by grants from National Science Council of Taiwan to P.-C. L. Hou (NSC 89-2621-B-006-005-A10 and NSC 90-2621-B-006-005-A10).

LITERATURE CITED

AERTS, R. 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* 79:439–449.

BEARD, K. H., VOGT, K. A. & KULMATISKI, A. 2002. Top-down effects of a terrestrial frog on forest nutrient dynamics. *Oecologia* 133:583–593.

BEARD, K. H., ESCHTRUTH, A. K., VOGT, K. A., VOGT, D. J. & SCATENA, F. N. 2003. The effects of the frog *Eleutherodactylus coqui* on invertebrates and ecosystems processes at two scales in the Luquillo Experimental Forest, Puerto Rico. *Journal of Tropical Ecology* 19:607–617.

CALDWELL, J. P. & VITT, L. J. 1999. Dietary asymmetry in leaf litter frogs and lizards in a transitional northern Amazonian rain forest. *Oikos* 84:383–397.

CHEN, Z. S., HSIEH, C. F., JIANG, F. Y., HSIEH, T. H. & SUN, I. F. 1998. Relations of soil properties to topography and vegetation in a subtropical rain forest in southern Taiwan. *Plant Ecology* 132:229–241.

CLARKE, K. R. & WARWICK, R. M. 1994. *Change in marine communities: an approach to statistical analysis and interpretation*. Plymouth Marine Laboratory, Plymouth. 144 pp.

COLEMAN, D. C., CROSSLEY, D. A. & HENDRIX, P. F. 2004. *Fundamentals of soil ecology*. (Second edition). Elsevier Academic Press, Oxford. 386 pp.

COUTEAUX, M. M., BOTTNER, P. & BERG, B. 1995. Litter decomposition, climate and litter quality. *Trends in Ecology and Evolution* 10:63–66.

EDWARDS, C. A. & BOHLEN, P. J. 1996. *Biology and ecology of earthworms*. Chapman & Hall, New York. 426 pp.

GONZÁLEZ, G. & SEASTEDT, T. R. 2000. Comparison of the abundance and composition of litter fauna in tropical and subalpine forests. *Pedobiologia* 44:545–555.

GONZÁLEZ, G. & SEASTEDT, T. R. 2001. Soil fauna and plant litter decomposition in tropical and subalpine forests. *Ecology* 82:955–964.

HOU, P.-C. L., ZOU, X., HUANG, C.-Y. & CHIEN, H.-J. 2005. Plant litter decomposition influenced by soil animals and disturbance in a subtropical rainforest of Taiwan. *Pedobiologia* 49:539–547.

HOULAHAN, J. E., FINDLAY, C. S., SCHMIDT, B. R., MEYER, A. H. & KUZMIN, S. L. 2000. Quantitative evidence for global amphibian population declines. *Nature* 404:752–755.

HUANG, C.-Y. & HOU, P.-C. 2004. Density and diversity of litter amphibians in a monsoon forest of southern Taiwan. *Zoological Studies* 43:795–802.

KAJAK, A. & JAKUBCZYK, H. 1977. Experimental studies on predation in the soil-litter interface. Pp. 493–496 in Lohm, U. & Persson, T. (ed.). *Soil organisms as components of ecosystems*. Ecological Bulletin 25. Swedish Natural Science Research Council, Stockholm.

KLEEBERGER, S. R. & WERNER, J. K. 1982. Home range and homing behavior of *Plethodon cinereus* in Northern Michigan. *Copeia* 2:409–415.

LIMA, A. P., MAGNUSSON, W. E. & WILLIAMS, D. G. 2000. Differences in diet among frogs and lizards coexisting in subtropical forests of Australia. *Journal of Herpetology* 34:40–46.

LIPS, K. R. 1998. Decline of a tropical montane amphibian fauna. *Conservation Biology* 12:106–117.

MUNSON, R. D. & NELSON, W. L. 1990. Principle and practices in plant analysis. Pp. 359–387 in Westerma, R. L. (ed.). *Soil testing and plant analysis*. Soil Science Society of America, Madison.

REDDY, M. V. & VENKATAIAH, B. 1989. Influence of microarthropod abundance and climatic factors on weight loss and mineral nutrient contents of *Eucalyptus* leaf litter during decomposition. *Biology and Fertility of Soils* 8:319–324.

ROONEY, T. P., ANTOLIK, C. & MORAN, M. D. 2000. The impact of salamander predation on collembola abundance. *Proceedings of the Entomological Society of Washington* 102:308–312.

SIMON, M. P. & TOFT, C. A. 1991. Diet specialization in small vertebrates: mite-eating in frogs. *Oikos* 61:263–278.

STEWART, M. M. & WOOLBRIGHT, L. L. 1996. Amphibians. Pp. 273–320 in Reagan, D. P. & Waide, R. B. (ed.). *The food web of a tropical rain forest*. The University of Chicago Press, Chicago.

SUN, I.-F., HSIEH, C.-F. & HUBBELL, S. P. 1998. The structure and species composition of a subtropical monsoon forest in southern Taiwan on a steep wind-stress gradient. Pp. 147–169 in Turner, I. M., Diong, C. H., Lim, S. S. L. & Ng, P. K. L. (ed.). *Biodiversity and the dynamics of ecosystems*. DIWPA, Kyoto.

TAIGEN, T. L. & POUGH, F. H. 1983. Pery preference, foraging behavior, and metabolic characteristics of frogs. *American Naturalist* 122:509–520.

TOFT, C. A. 1980. Feeding ecology of thirteen syntopic species of anurans in a seasonal tropical environment. *Oecologia* 45:131–141.

TSUI, C.-C., CHEN, Z.-S. & HSIEH, C. F. 2004. Relationships between soil properties and slope position in a lowland rain forest of southern Taiwan. *Geoderma* 123:131–142.

VITOUSEK, P. M. & SANFORD, R. L. 1986. Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics* 17:137–167.

WARDLE, D. A. & LAVELLE, P. 1997. Linkages between soil biota, plant litter quality and decomposition. Pp. 107–124 in Cadisch, G. & Giller, K. E. (ed.). *Driven by nature*. CAB International, Wallingford.

WISE, D. H. 2004. Wandering spiders limit densities of a major microbi-detrivore in the forest-floor web. *Pedobiologia* 48:181–188.

WOLTERS, V. & EKSCHMITT, K. 1977. Gastropods, isopods, diplopods, and chilopods: neglected groups of the decomposer food web. Pp. 265–306 in Benckiser, G.. (ed.). *Fauna in soil ecosystems: recycling processes, nutrient fluxes, and agricultural production*. Marcel Dekker, New York.

WYMAN, R. L. 1998. Experimental assessment of salamanders as predators of detrital food webs: effects on invertebrates, decomposition and the carbon cycle. *Biodiversity and Conservation* 7:641–650.