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Effects of Greenfall on Ground-dwelling Arthropods in a Subtropical Forest

Chien-Lung Chen and Pei-Jen L. Shaner*

Department of Life Science, National Taiwan Normal University, Taipei, Taiwan 11677. E-mail: archerdragon781203@livemail.tw (Chen)

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Chien-Lung Chen and Pei-Jen L. Shaner (2018) Resource events such as typhoon-triggered greenfall have consequences for multiple ecological mechanisms, ranging from population dynamics and trophic interactions to ecosystem processes. Arthropods are sensitive to environmental disturbances, and many taxa have been used as indicator species. In a field experiment, we tested the effects of greenfall on ground-dwelling arthropods (mostly litter-dwelling taxa) in a forest of Taiwan red pine (*Pinus taiwanensis*) in the summer of 2013. Of 20 field plots (5 × 5 m), half received *P. taiwanensis* greenfall while the other half served as unaltered controls. As predicted, some arthropod taxa responded more strongly than others to the greenfall addition. Among the examined arthropod taxa (Araneae, Coleoptera: Carabidae, Coleoptera: Staphylinidae, Hymenoptera: Formicidae, Collembola, Isopoda: Oniscidea), the predatory staphylid beetles (Staphylinidae) responded positively to greenfall addition while the larger-sized detritivore woodlice (Oniscidea) responded negatively. Contrary to our prediction of a positive response, the smaller-sized detritivore springtails (Collembola) were unaffected by the greenfall addition. At the beginning of this study, we observed short-term effects of a naturally-occurring typhoon, to which springtails and ants (Formicidae) responded negatively while staphylid beetles responded positively. Also contrary to our prediction, these taxon-specific responses did not suffice to alter the composition of arthropod communities. We concluded that the intra-annual effects of typhoons-specifically those associated with greenfall-are more likely to impact certain taxa, including staphylid beetles, woodlice, springtails and ants. At the taxonomic level examined here, these intra-annual effects on community composition are non-detectable. As typhoon frequency and intensity are likely to change with global warming, the study makes a timely contribution to our understanding of typhoon-induced ecological dynamics in subtropical plantation forests.

Key words: Litterfall, Resource event, Rove beetles, Tropical cyclone, Typhoon.

BACKGROUND

Resource events have consequences for multiple ecological mechanisms, ranging from population dynamics to trophic interactions and ecosystem processes (McShea 2000; Stapp and Polis 2003; Schmidt and Ostfeld 2008). Pulse resource events are well recognized across ecosystems in the mass production of flowers and fruits or seeds (*e.g.*, Curran and Leighton 2000; McShea 2000), insect outbreaks (*e.g.*, Carlton and Goldman 1984; Haney 1999; Yang 2004), inputs of animal carcasses, dung or urine (*e.g.*, Peek and Forseth 2003; Wilmers et al. 2003), and typhoon-triggered greenfall (*e.g.*, Lodge et al. 1994). As a similar resource event can have different ecological consequences in different regions (Kelly et al. 2008), empirical evidence from different ecosystems can contribute significantly to our overall understanding of ecological dynamics

*Correspondence: E-mail: pshaner@ntnu.edu.tw

driven by resource events (Yang et al. 2010).

Typhoons are tropical cyclones, which can cause substantial physical damage to trees (Whigham et al. 1991; Boose et al. 1994) and create greenfall resource pulses (Lodge et al. 1994). Greenfall mainly comprises nutrient-rich fresh or immature leaves, in contrast to aging leaves, whose nutrients are translocated to other tissues prior to falling (Lodge et al. 1991; Whigham et al. 1991; Fonte and Schowalter 2004). Studies in Hong Kong, Japan and Taiwan have shown that typhoons can contribute 20-50% of annual litterfall (Lam and Dudgeon 1985; Lin et al. 2003; Xu et al. 2004). Similarly, in the montane rainforests of Puerto Rico, greenfall generated by hurricanes has been shown to create an influx of nutrients to the litter layer of more than twice the annual average (Lodge et al. 1991). Despite these documented impacts, typhoon-triggered greenfall remains a rarely studied resource event for animal consumers (but see Schowalter et al. 2014).

Arthropods are sensitive to changes in their environment, and this makes them suitable indicator species for natural or anthropogenic perturbations (Lieberman and Dock 1982; Kremen 1992; Kremen et al. 1993). As ground-dwelling arthropods comprise tightly linked trophic groups (*e.g.*, detritivores, microbivores, predators) of varying body sizes, different taxa may respond differently to a given resource event (Uetz 1979; Sayer 2005; Ober and DeGroote 2011). Litter provides food resources and serves as a habitat for ground-dwelling (and particularly litter-dwelling) arthropods. Specifically, the depth and structural complexity of the litter layer have been found to influence the abundance of spiders, beetles, centipedes, springtails and mites (*e.g.*, Gill 1969; Uetz 1979; Poser 1990; Magura et al. 2005; Sayer 2005). For instance, a thick litter layer of high structural complexity is often associated with increased abundance of arthropods, especially prey species with smaller body sizes, such as springtails (Collembola). This is probably because a thick litter offers more habitat space and shelter from predators and serves as a buffer against fluctuations in temperature and humidity (*e.g.*, Gill 1969; Sayer 2005; Yang et al. 2007; Ober and DeGroote 2011).

The effects of litter addition on predatory and omnivorous species or on larger-sized prey species are; however, more difficult to predict. While an increased volume of litter may provide more prey for predatory and omnivorous species, a complex litter structure may provide more shelter for those prey, making it difficult for predatory or omnivorous species to capture them-for example, increased litter depth reduces caterpillar mortality by ant predation (Karban et al. 2013). Several studies reported higher abundance of spiders (Araneae), carabid beetles (Coleoptera) and Arachnida in litter-addition plots (Uetz 1979; Magura et al. 2005; Sayer 2005) while Ober and DeGroote (2011) found higher abundance of spiders and ants (Hymenoptera: Formicinae) in litter-removal plots. Larger-sized prey, such as woodlice (Isopoda), may exhibit a complex relationship with litter addition, as the benefits of additional litter (more habitat space, increased shelter from predators, buffering against micro-climates) may not suffice to offset the increased risk if predators respond positively to litter addition. Given the possible taxon-specific responses to changes in litter qualities and/or quantities, arthropod community composition is likely to be altered by litter addition or removal.

The quantity and quality of greenfall triggered by typhoons varies by forest type. For example, Wang et al. (2013) compared litterfall dynamics in a natural hardwood forest and a plantation forest of Chinese fir (*Cunninghamia lanceolata*) in Taiwan, both of which were exposed to the same four typhoons in 2008. In the Chinese fir plantation, the impact of these typhoons contributed 81% of the annual litterfall (6000 out of 7400 kg ha^{-1}); in the natural hardwood forest, the typhoons contributed 59% of the annual litterfall (6630 out of 11400 kg ha^{-1}). Additionally, the typhoons contributed approximately 80% and 60% of litterfall nutrient flux in the Chinese fir plantation and natural hardwood forest, respectively. This suggests that typhoon-triggered greenfall plays an important role in litter layer nutrient cycling, particularly in plantation forests. By 2000, forest plantations accounted for 16% of forest cover in the Asia-Pacific region or 61% of the world's plantation forests (FAO 2004). As forest plantations continue to replace natural forests as the primary source of wood products, the area covered by forest plantations is projected to increase in the future (FAO 2004), and there is an urgent need for more empirical studies of ecological processes in plantation forests.

The purpose of the present study is to investigate the effects of greenfall on ground-dwelling arthropods in a plantation forest of Taiwan red pine (*Pinus taiwanensis*). Plantation forests currently account for 20% of Taiwan's forest cover (Taiwan Forestry Bureau), and typhoons are one of the main drivers of litterfall dynamics (Lin et al. 2003; Wang et al. 2013). For the purposes of this study, we created an artificial greenfall event that might have been generated by typhoons and monitored changes in arthropod abundance and composition over a period of six months. We hypothesized that greenfall addition would have positive effects on ground-dwelling arthropods by providing more habitat space, shelter from predators and/or shelter against unfavorable climatic conditions. However, we expected that some taxa (such as smaller-sized detritivores) would respond more strongly than others because they are more likely to benefit from additional shelter and may even use greenfall directly as a food resource. Given these potential taxon-specific responses, we also hypothesized that arthropod community composition would be altered by greenfall addition.

MATERIALS AND METHODS

Study site

The study was conducted at a Taiwan red pine (*Pinus taiwanensis*) plantation forest in the montane region of central Taiwan (121°18'E, 24°21'N; elevation 1800-2000 m), where the dominant understory species is *Miscanthus transmorrisonensis* Hayata. Annual precipitation is 1100 mm and mean temperature is 13°C (lowest in January at 5°C and highest in July at 19°C). On average, central Taiwan experiences one typhoon per year (Wang et al. 2013).

Greenfall addition

The site was sloping, so we set up 10 pairs of 5 × 5 m plots (20 plots in total). One plot in each pair was randomly assigned to receive greenfall (the experimental plot) while the other served as a control plot. The distance between any two neighboring plots was at least 50 m, and all plots were at least 10 m from the forest edge. On 7 July 2013, each experimental plot received 10 kg of fresh *P. taiwanensis* greenfall to simulate greenfall generated by a typhoon; this greenfall was freshly collected from a nearby *P. taiwanensis* forest by manually cutting small branches from the canopy layer. At a nearby Chinese fir plantation (*c.* 68 km from the study site), the accumulated greenfall from four consecutive typhoons between July and September 2008 was *c*. 6000 kg ha^{-1} (Wang et al. 2013). The amount of greenfall caused by a single typhoon can vary significantly (*c*. 1000-2000 kg ha^{-1}; Wang et al. 2013). For this purpose, we used a one-time greenfall addition of 4000 kg ha^{-1} (10 kg per 25 m^2 plot), which is at the upper end of typhoon-generated greenfall.

On 13 July, one week after greenfall addition, the study site was hit by Typhoon Soulik (maximum wind speed 38 m s^{-1}; precipitation 307 mm at Lishan weather station *c*. 13 km from the study site; Taiwan Central Weather Bureau Typhoon DateBase). On 18 July, we removed all fresh greenfall from the control plots but left the additional, typhoon-induced greenfall on the experimental plots. Although we did not directly measure the amount of greenfall caused by Typhoon Soulik, we estimated this as *c*. 1000-2000 kg ha^{-1} because the intensity of Typhoon Soulik fell within the range of the four typhoons reported in Wang et al. (2013). Even with our additional greenfall, then, the total was unlikely to exceed the natural level of *c*. 6000 kg ha^{-1} for this region.

Arthropod sampling

Arthropods were sampled using pitfall traps: three within each plot, with a minimum distance of 1 m between traps. Each trap comprised a 50 ml centrifuge tube (11.5 cm in depth, 3 cm in diameter), with a small plastic cover (8 cm in diameter) placed 5 cm above the trap to prevent rain water from entering. Each trap was filled with 25 ml of 4% formaldehyde solution and a few drops of unscented dish detergent as interface agent to reduce surface tension. Traps were buried to a depth that left the top of the tube flush with the ground surface. The traps were set on 12 May 2013, and we collected samples every 15 ± 3 days until 26 December (15 sampling events in total). After transporting the samples back to the laboratory, we gently rinsed them with clean water in a mesh sieve (0.420 m/m opening) to remove soil. The remnants were then stored in 75% ethanol for taxonomic identification. Arthropods were classified to order or family level, based on their morphology under a dissecting microscope (10× ocular lens with 0.8× - 5× objective lens). After counting the number of individuals in each taxonomic group, all were oven-dried at 60°C to to make their weights constant for biomass estimates.

Data analysis

To produce plot-level measures, the

arthropods' activity density (*i.e.*, number of individuals) and biomass (*i.e.*, dry weight) were averaged across the three pitfall traps. We used averages rather than sums because there were a few cases of missing data due to animal disturbances. Activity density and biomass values were combined across sampling events into three time periods-pre-treatment (12 May-7 July), post-treatment #1 (24 July-10 October), and post-treatment #2 (10 October-27 December)-based on seasonal typhoon patterns in Taiwan. Of 58 typhoons that passed through central Taiwan from 1958 to 2015, 97% occurred between 7 July and 10 October while only 2% occurred between 10 October and 27 December (Taiwan Central Weather Bureau Typhoon DateBase). It follows that arthropods at the study site typically experience typhoons during post-treatment time period #1 rather than post-treatment time period #2. We chose to assign the samples to these three time periods because it is ecologically meaningful (with a logistics-based sampling interval of 15 ± 3 days) and reduces random temporal variations. The samples for 7 July-24 July were set aside for separate testing, treating Typhoon Soulik as a natural experiment. Because all plots were temporarily affected by Typhoon Soulik during that period, we assigned these samples to the 'after Soulik' group while samples taken between 24 June and 7 July were used as the 'before Soulik' control. Prior to statistical analyses, activity density and biomass values were standardized, based on the unit 'number trap^{-1}' or 'mg trap^{-1}' (both over a period of 15 days).

Although we identified all captured arthropods, we focused on the following six taxa for univariate analysis: spiders (Araneae), carabid beetles (Coleoptera: Carabidae, tentatively identified as *Pterostichus* sp.), staphylid beetles (Coleoptera: Staphylinidae), ants (Hymenoptera: Formicidae), springtails (Collembola) and woodlice (Isopoda: Oniscidea). These six taxa, which belong to two major trophic groups (detritivores and consumers; see Table 1), were sufficiently abundant at the study site to allow taxon-specific model fitting. For each arthropod taxon, generalized linear mixed models (GLMMs) with Poisson distribution were used to test the effects of greenfall addition or of Typhoon Soulik on activity density and biomass. In the case of artificial addition, we treated greenfall treatment, time period (*i.e.*, pre-treatment, post-treatment #1, post-treatment #2) and their interaction as fixed effects, with each plot repeatedly measured across the three time periods as a random effect. For Typhoon Soulik, greenfall treatment, typhoon (*i.e.*, before vs. after Soulik) and their interaction were treated as fixed effects, with each plot repeatedly measured before and after the typhoon as a random effect. The pairing of plots (*i.e.*, 10 pairs arranged along the slope) was initially treated as a block factor. However, as this failed to explain a significant amount of variation, it was subsequently removed from the models.

To assess the effects of greenfall addition or of Typhoon Soulik on arthropod community composition, we included three additional taxa: mites (Arachnida: Acari), centipedes (Chilopoda: Scolopendromorph) and crane flies (Diptera:

Table 1. Trophic groups of the arthropod taxa analyzed in this study. Stable carbon and nitrogen isotope values are based on the present study and a previous study at a nearby location (< 2 km from current study site; Shaner et al. 2013). *Pinus taiwanensis*, the dominant tree species at the study site and major component of the added greenfall, has a mean δ^{13}C = -28.6 ± 0.6 ‰ (SD) and δ^{15}N = -3.9 ± 1.1‰ (N = 3). *Miscanthus transmorrisonensis* Hayata, the dominant understory species, has a mean δ^{13}C = -13.0 ± 0.3‰ and δ^{15}N = -3.3 ± 0.3‰ (N = 3). Given the small body size of the arthropods (with the exception of carabid beetles and woodlice), multiple individuals from the same plot were pooled across pitfall traps and sampling time periods to create a replicate. Although isotope data are not available for staphylid beetles, they are most likely predatory consumers (Bohac 1999; Barton et al. 2011)

Taxa	Common name	Trophic role	δ^{13}C‰ (mean ± SD)	δ^{15}N‰ (mean ± SD)
Collembola	Springtail	Detritivore	-25.2 ± 0.5 (*n* = 3)	0.2 ± 1.1 (*n* = 3)
Isopoda: Oniscidea	Woodlouse	Detritivore	-24.0 ± 0.8 (*n* = 21)	0.4 ± 1.8 (*n* = 21)
Araneae	Spider	Consumer	-23.3 ± 1.0 (*n* = 29)	4.7 ± 1.5 (*n* = 29)
Coleoptera: Carabidae (*Pterostichus* sp.)	Carabid beetle	Consumer	-26.0 ± 2.3 (*n* = 2)	4.7 ± 1.2 (*n* = 2)
Coleoptera: Staphylinidae	Staphylid beetle	Consumer	NA	NA
Hymenoptera: Formicidae	Ant	Consumer	-23.7 ± 1.4 (*n* = 4)	3.8 ± 2.7 (*n* = 4)

Tipulidae). All nine taxa included in the community composition analysis had an accumulated count of at least 100 individuals during the study period. To compare arthropod community composition across treatment plots and time periods, we used non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity matrices (Ober and DeGroote 2011). The analysis included 60 sample units (*i.e.*, 20 plots × three time periods) for artificial greenfall addition and 40 sample units (*i.e.*, 20 plots × two time periods) for Typhoon Soulik. Two gradients were extracted from NMDS, and all sample units were plotted on the two-dimensional space to visualize the degree of dissimilarity in arthropod community composition for control and greenfall plots and for before- and after-Soulik time periods.

All statistics were performed in R 3.3.2; the GLMMs were performed in SAS 9.4.

RESULTS

We collected 43,949 arthropods from 20 taxa; the six analyzed for taxon-specific effects were well represented in the samples (*activity density*: spiders 3.7%, carabid beetles 1.5%, staphylid beetles 2.6%, ants 1.4%, springtails 85.8%, woodlice 0.7%; *biomass*: spiders 2.0%, carabid beetles 39.8%, staphylid beetles 0.3%, ants 0.3%, springtails 1.3%, woodlice 0.2%). The three additional taxa included in the community composition analysis were also prevalent in the samples (*activity density*: mites 3.1%, centipedes 0.3%, crane flies 0.4%; *biomass*: mites 0.3%, centipedes 0.3%, crane flies 0.2%).

Two of the six taxa responded to greenfall addition (Table 2; Fig. 1); in particular, the staphylid beetles exhibited higher activity densities in the greenfall plots during post-treatment time period #2 while the woodlice exhibited lower activity-densities in the greenfall plots during post-treatment period #1 (Fig. 1). After Typhoon Soulik, springtail activity density and biomass decreased in both control and greenfall plots (Table 3; Fig. 2). Ant biomass also decreased after the typhoon, especially in the greenfall plots (Table 3; Fig. 2). The biomass of staphylid beetles increased after the typhoon, but this occurred only in the control plots (Table 3; Fig. 2).

For both artificial greenfall addition and Typhoon Soulik, the NMDS with two gradients

Table 2. Effects of the greenfall addition on arthropod activity-density and biomass. The ‘greenfall’ effect includes the control and greenfall plots. The ‘time’ effect includes one pre-treatment period (12 May-7 July) and two post-treatment periods (24 July-10 October, 10 October-27 December). The ‘Num DF’ and ‘Den DF’ denote the ‘numerator degree of freedom’ and ‘denominator degree of freedom’ for the *F* statistic respectively. Significant effects in bold

				Activity-density		Biomass	
Taxa	Effect	Num DF	Den DF	*F*	*P*	*F*	*P*
Spiders	Greenfall	1	18	0.42	0.53	0.05	0.83
	Time	2	36	27.05	**< .0001**	5.66	**0.01**
	Greenfall × time	2	36	0.11	0.90	1.72	0.19
Carabid beetles	Greenfall	1	18	0.27	0.61	0.21	0.65
	Time	2	36	15.34	**< .0001**	15.84	**< .0001**
	Greenfall × time	2	36	0.12	0.89	0.15	0.86
Staphylid beetles	Greenfall	1	18	4.23	**0.05**	0.31	0.59
	Time	2	36	5.64	**0.007**	4.95	**0.01**
	Greenfall × time	2	36	1.96	0.16	0.45	0.64
Ants	Greenfall	1	18	0.30	0.59	0.70	0.41
	Time	2	36	29.10	**< .0001**	8.44	**0.001**
	Greenfall × time	2	36	0.31	0.73	0.08	0.92
Springtails	Greenfall	1	18	0.87	0.36	0.74	0.40
	Time	2	36	3.31	**0.05**	11.74	**0.0001**
	Greenfall × time	2	36	1.28	0.29	0.69	0.51
Woodlice	Greenfall	1	18	3.70	0.07	3.58	0.07
	Time	2	36	3.96	**0.03**	6.53	**0.004**
	Greenfall × time	2	36	0.79	0.46	0.33	0.72

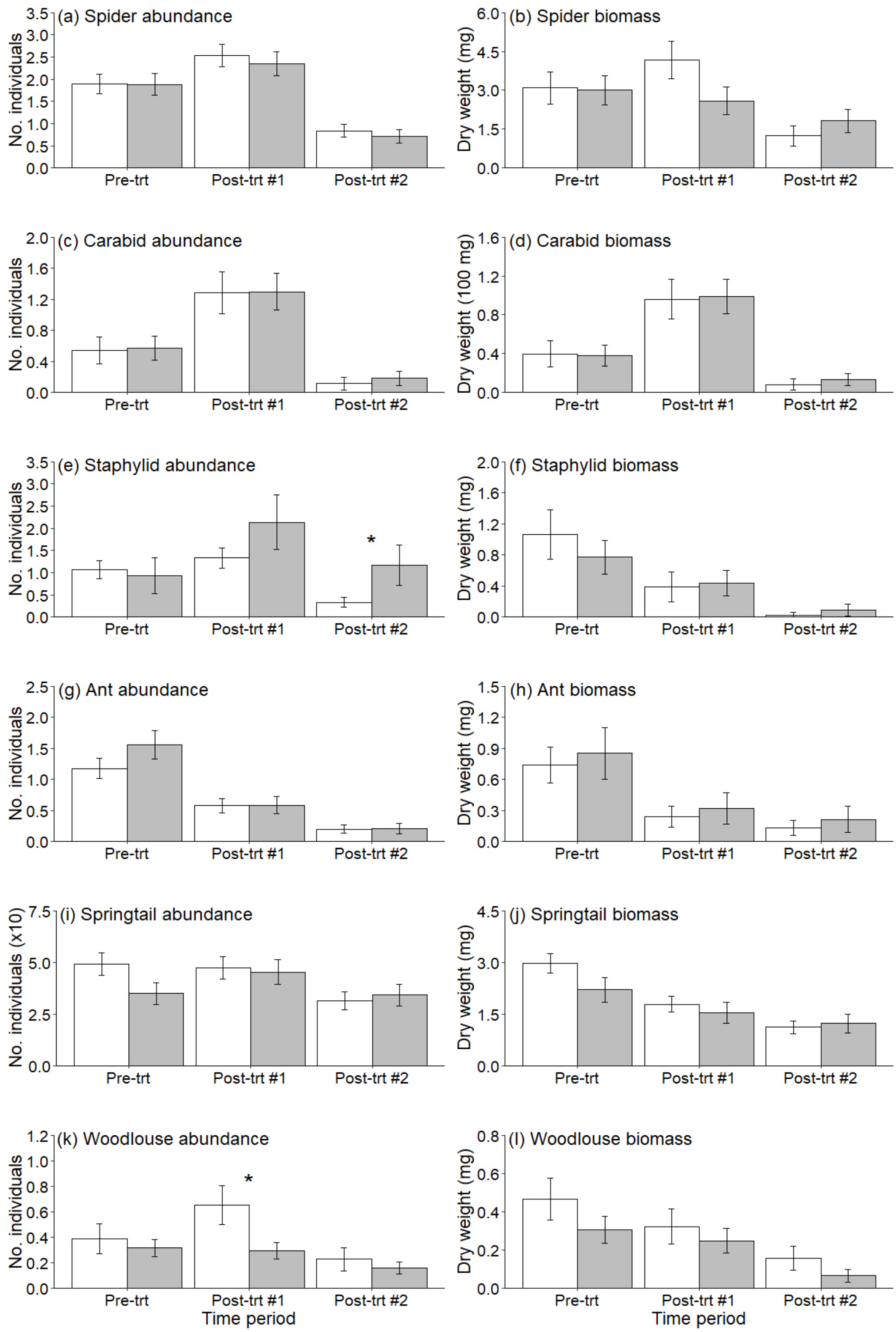

Fig. 1. Activity-density and biomass of six arthropod taxa in response to greenfall addition. The greenfall plots (gray bars) received greenfall addition during the two post-treatment periods (post-treatment time period #1: 24 July-10 October, post-treatment time period #2: 10 October-27 December). The pre-treatment period is 12 May-7 July. The control plots (white bars) did not received greenfall addition in any of three time periods. The asterisks denote significant differences in arthropod activity-density between greenfall and control plots for a given time period.

had an acceptable stress value of 0.2. The large overlapping areas on the two-dimensional space between control and greenfall plots (Fig. 3) and before and after Typhoon Soulik (Fig. 4) suggest that arthropod community composition was unaltered by either artificial greenfall addition or typhoon disturbance.

DISCUSSION

As staphylid beetles are primarily predatory (ranging from active hunters to scavengers; Bohac 1999; Barton et al. 2011) and do not directly consume greenfall, their positive responses to greenfall may be an effect of increased prey, habitat space and shelter number. Indeed, forests where understory vegetation is less disturbed have been found to exhibit higher staphylid activity densities (Fellin 1980; Pohl et al. 2007). Although we did not quantify the thickness or structural complexity of the litter layer at the study site, it is clear from visual inspection that the greenfall plots show higher habitat complexity immediately after greenfall addition (Fig. S1).

Woodlice are decomposers that feed primarily on decaying plant litter. However, in the case of pine needles, woodlice tend to favor decayed rather than fresh litter (Soma and Saito 1983; Zimmer 2002), which means that they may not view the fresh greenfall following a typhoon as a high quality food resource. Alternatively, assuming that greenfall was consumed by the woodlice, they might reduce their activities in response to the greenfall subsidy. Additionally, as woodlice are prey for many small mammals and invertebrate predators (*e.g.*, spiders, centipedes, beetles; Sutton 1970), increased predation pressure as a result of their predators' positive responses to greenfall might lead to decreased woodlice activity density or biomass.

The negative responses of springtails and ants to Typhoon Soulik (but not to greenfall addition) suggests non-greenfall effects. Typhoons bring precipitation to the forest floor, and soil water content is known to affect springtail and ant abundances (Chikoski et al. 2006). Specifically, higher soil water content was found to increase springtail abundance and reduce ant abundance (Chikoski et al. 2006), and the latter may explain

Table 3. Effects of Typhoon Soulik on arthropod activity-density and biomass. The 'greenfall' effect includes the control and greenfall plots, and the 'typhoon' effect includes the before-Soulik (24 June-7 July) and after-Soulik (7 July-24 July) time periods. All plots were under the influence of the typhoon during the after-Soulik period. However, the greenfall plots received additional greenfall before the typhoon. The 'Num DF' and 'Den DF' denote the 'numerator degree of freedom' and 'denominator degree of freedom' for the *F* statistic respectively. Significant effects in bold

				Activity-density		Biomass	
Taxa	Effect	Num DF	Den DF	*F*	*P*	*F*	*P*
Spiders	Greenfall	1	18	0.55	0.47	0.14	0.71
	Typhoon	1	18	0.53	0.48	0.98	0.33
	Greenfall × typhoon	1	18	0.01	0.92	0.35	0.56
Carabid beetles	Greenfall	1	18	0.00	0.99	0.06	0.81
	Typhoon	1	18	0.27	0.61	0.01	0.90
	Greenfall × typhoon	1	18	0.20	0.66	0.13	0.72
Staphylid beetles	Greenfall	1	18	0.51	0.48	1.38	0.26
	Typhoon	1	18	2.32	0.14	0.60	0.45
	Greenfall × typhoon	1	18	0.01	0.92	6.53	**0.02**
Ants	Greenfall	1	18	0.55	0.47	2.10	0.16
	Typhoon	1	18	0.48	0.50	4.39	**0.05**
	Greenfall × typhoon	1	18	0.29	0.59	2.14	0.16
Springtails	Greenfall	1	18	0.01	0.94	0.76	0.39
	Typhoon	1	18	12.47	**0.002**	21.99	**0.0002**
	Greenfall × typhoon	1	18	0.38	0.55	0.24	0.63
Woodlice	Greenfall	1	18	0.12	0.74	0.05	0.82
	Typhoon	1	18	1.70	0.21	2.69	0.12
	Greenfall × typhoon	1	18	0.02	0.88	0.38	0.54

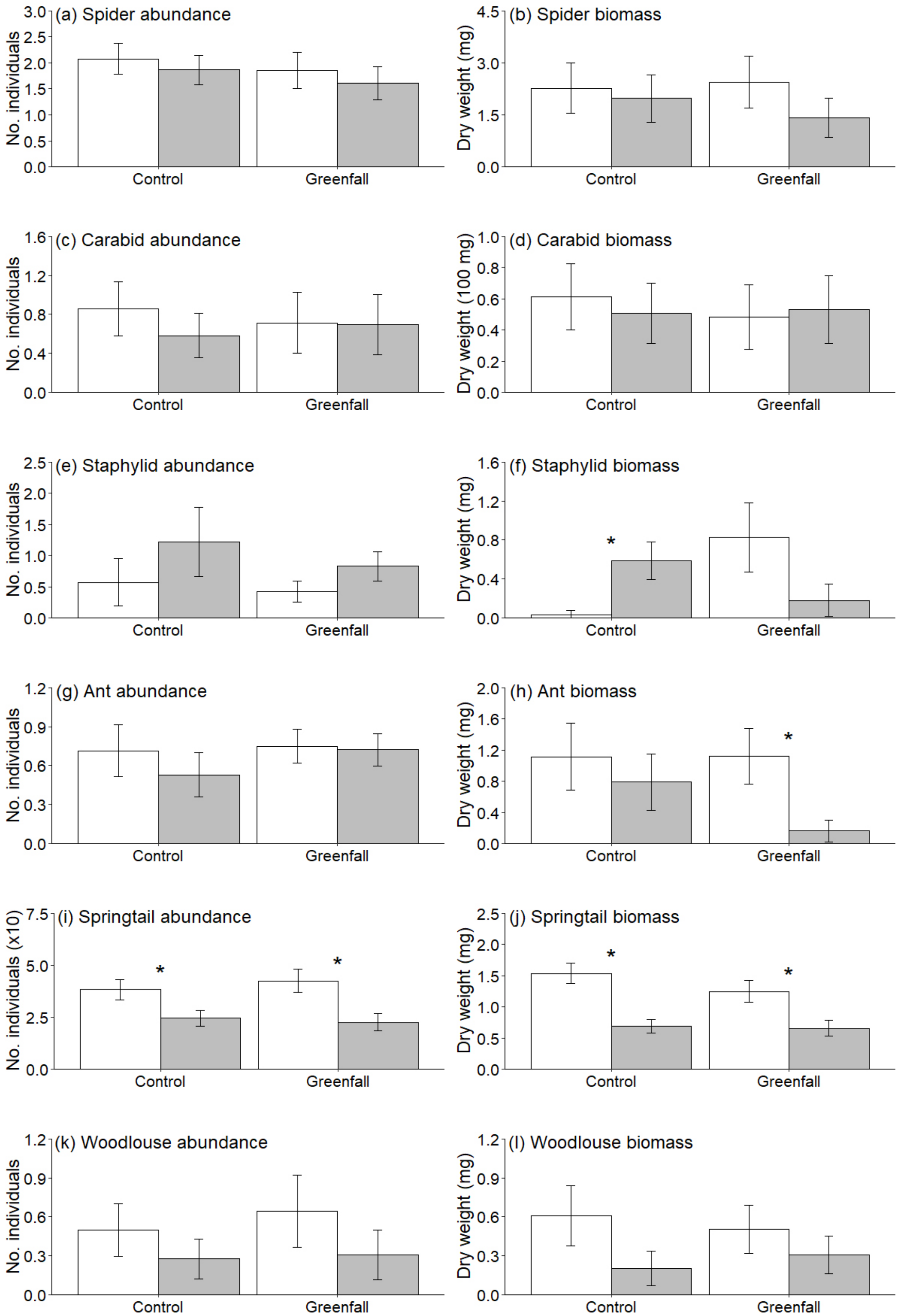

Fig. 2. Activity-density and biomass of six arthropod taxa in response to Typhoon Soulik. The white and gray bars denote the 'before Soulik' (24 June-7 July) and 'after Soulik' (7 July-24 July) periods, respectively. The arthropod data were pooled across all 20 plots, including the control and greenfall plots. Both the control and greenfall plots received the greenfall and other impacts from Typhoon Soulik during 'after Soulik' period. The greenfall plots received additional greenfall during both 'before Soulik' and 'after Soulik' periods. The asterisks denote significant differences in activity-density or biomass of the arthropods before and after Typhoon Soulik.

the ants' negative response to Typhoon Soulik. In addition to the impact of abiotic characteristics of the litter and soil layer (*e.g.*, moisture, temperature), springtails are also prey for certain ants (*e.g.*, Reznikova and Panteleeva 2001), beetles (*e.g.*, Ernsting 1977) and spiders (*e.g.*, Kuusk and Ekbom 2010). For that reason, springtail abundance may decrease because of other biotic factors, even when a typhoon beneficially alters some aspects of the environment (*e.g.*, soil water content).

It is possible that in manually removing typhoon-induced greenfall from the control plots on

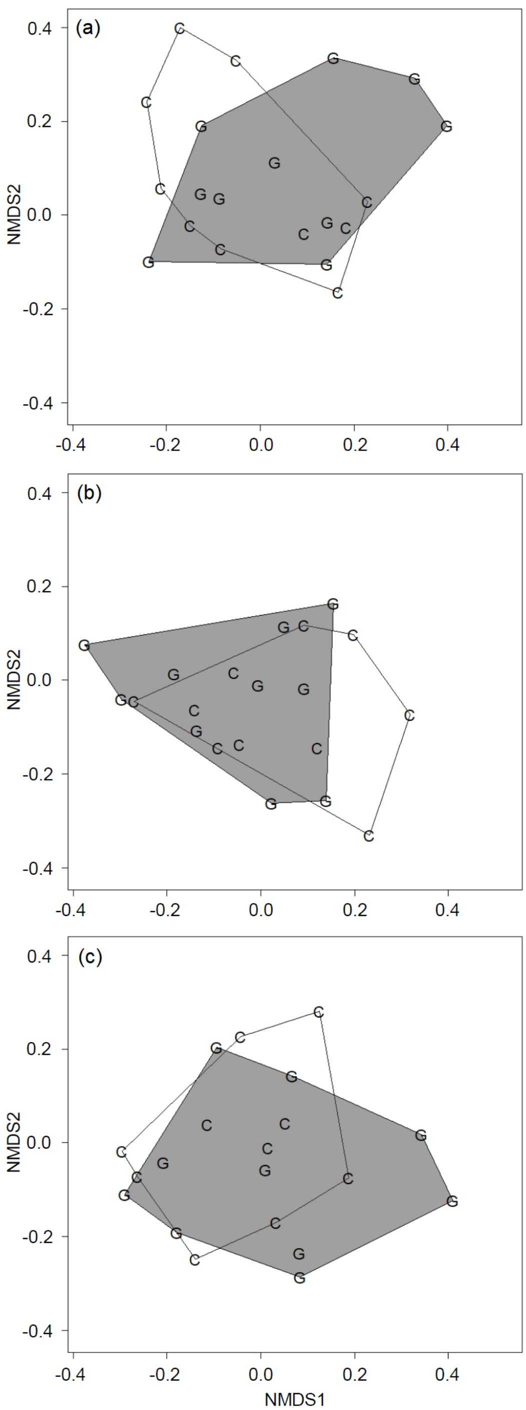

Fig. 3. NMDS biplot of arthropod communities in response to greenfall addition. (a) Pre-treatment, 12 May-7 July, (b) Post-treatment time period #1, 24 July-10 October, (c) Post-treatment time period #2, 10 October-27 December. The letter 'C' denotes a control plot and 'G' a greenfall plot. The unfilled and filled convex polygons denote the control and greenfall plots, respectively. Although the NMDS was performed on all 60 sample units (20 plots × three time periods), the biplot is drawn for each time period to enhance visual clarity. The scale and range of the axes are comparable across the three time periods.

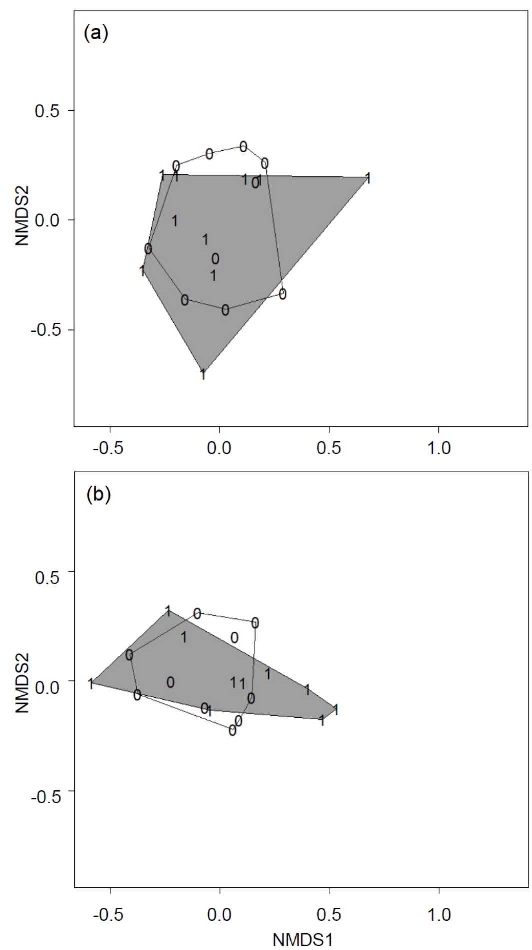

Fig. 4. NMDS biplot of arthropod communities in response to Typhoon Soulik. (a) Control plots, (b) Greenfall plots. The number '0' denotes a plot before Typhoon Soulik (24 June-7 July) and '1' a plot after Typhoon Soulik (7 July-24 July). The unfilled and filled convex polygons denote the 'before-Soulik' and 'after-Soulik' periods respectively. Although the NMDS was performed on all 40 sample units (20 plots × two time periods), the biplot is drawn for the control and greenfall plots separately to enhance visual clarity. The scale and range of the axes are comparable between the control and green plots.

18 July, we introduced some physical disturbance to the forest floor of those plots. However, the modest plot size (10 × 10 m) and the small visible amounts of typhoon-induced greenfall meant that one person could remove that typhoon-induced greenfall from all 10 control plots in one day, helping to minimize human disturbance of the forest floor. More importantly, in analyzing the effects of Typhoon Soulik, we pooled the data from the greenfall and control plots and compared only before- and after-Soulik samples. Human disturbance would have only occurred in half of the after-Soulik samples and was therefore less likely to have caused the overall negative responses of springtails and ants to Typhoon Soulik. We did not introduce the same human disturbance to greenfall plots on 18 July because that might increase its contribution to any differences between before- and after-Soulik samples. Compared to the level of human disturbance from greenfall addition early in the study (greenfall plots) and the 15 pitfall sampling events (all plots) throughout the study, we believe this one-time human disturbance to control plots was unlikely to account for overall patterns among the arthropods. Nevertheless, it is important to note that the control plots were subject to more human disturbance early in the study, and our findings should be interpreted with this in mind. In particular, caution is needed in relation to those Typhoon Soulik effects that occurred only for the control plots (*e.g.*, the increased biomass of staphylid beetles after the typhoon, which occurred only in the control plots).

The study has some limitations. First, the findings mainly reflect the intra-annual effects of greenfall. Although the added greenfall was visually undetectable toward the end of the study (Fig. S1), and a recent study in a tropical forest (Schowalter et al. 2011) has shown that greenfall had smaller effects on forest floor nutrient fluxes than throughfall and frassfall (insect feces), it remains possible that greenfall has inter-annual effects as it enters the soil layer. For instance, Schowalter et al. (2014) reported that the addition of greenfall ('debris') from canopy trimming to the forest floor had an effect on canopy arthropods, suggesting potential indirect effects of greenfall on nutrient availability for trees when producing new foliage. It follows that greenfall's effects on arthropods may not be confined to the forest floor. Second, as we were unable to analyze the arthropod data at a finer taxonomic level (genus or species), the lack of response in relation to arthropod community composition may reflect the coarse taxonomic resolution. Different arthropod species within a given taxon may respond positively or negatively to litter manipulation (*e.g.*, Uetz 1979; Sayer 2005; Ober and DeGroote 2011; Schowalter et al. 2014). For example, relative abundance of Lycosidae was found to decrease with increasing litter depth and complexity while relative abundance of Clubionidae, Thomisidae and Gnaphosidae increased (Uetz 1979), which we would have missed in this study. However, we are fairly confident that there was a true lack of response among carabid beetles, because all examined specimens were tentatively identified as *Pterostichus* sp. Finally, because we used traps of relatively small (3 cm) diameter to avoid accidental fatalities among small vertebrates (*e.g.*, shrews, mice, frogs, lizards), large arthropods may be under-represented (Brown and Mathews 2016). That said, a 2012 survey using pitfall traps of much larger diameter (6.5 cm) found that a majority of common arthropod taxa at the study site had a body length less than 3 cm (with the exception of Chilopoda, which may exceed 6.5 cm; Table S1), which suggests that under-sampling of large arthropods is unlikely to be a serious issue.

CONCLUSIONS

This study provides empirical evidence on how ground-dwelling arthropods respond to a greenfall event. Greenfall is more nutritious and structurally more complex than litterfall, which mainly comprises aging leaves (*e.g.*, in deciduous forests; Lodge et al. 1991; Whigham et al. 1991). Therefore, studying the ecological consequences of greenfall can enhance our overall understanding of litterfall dynamics. Depending on forest type and typhoon characteristics, greenfall comprises branches and twigs of varying size and nutritional quality that may have complex effects on animal communities through biotic and abiotic interactions. As typhoon frequency and intensity are likely to change with global warming (Chan and Liu 2004), and as the area covered by plantation forest is likely to increase in the future (FAO 2004), this study makes a timely contribution to our understanding of typhoon-induced ecological dynamics in plantation forests.

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Authors' contributions: PLS conceived the research ideas. CLC and PLS designed the experiment. CLC performed the field and laboratory work. PLS analyzed the data. CLC and PLS wrote the manuscript.

Competing interests: CLC and PLS declare that they have no conflict of interest. PLS has received a research grant from Taiwan's Ministry of Science and Technology.

Availability of data and materials: Fig S1, Greenfall addition photos. Table S1, Arthropod body length. Additional file, Arthropod abundance and biomass.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

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Supplementary Materials

Fig. S1. Photos of the control and greenfall plots. The top four panels are one pair of the control and green plots (control #1, greenfall #1), and the lower four are a second pair (control #2, greenfall #2). The photos of 7 July 2013 were taken immediately after the greenfall addition, and the photos of 27 December 2013 were taken at the end of the study. (download)

Table S1. Body length of the arthropod taxa captured in a 2012 survey at current study site. Between June and September of 2012, six pitfall traps were set up at the study site. The pitfall traps were buried at a depth such that the top of the cup was flush with the surface of the ground. The traps were made of plastic cups (diameter = 6.5 cm, height = 4.8 cm) and filled with ~50 mL of water. In each of the four months (*i.e.* June, July, August, September), we opened the traps for three consecutive days. On each day, clean traps with water were set up in the evening and all captured arthropods were collected and brought back to the lab the next morning. The distance between any two pitfall traps was more than 20 m. Once brought back to the lab, we rinsed the specimen with water, identified them to order or family level based on their morphology under a microscope, and randomly selected 5-22 individuals for body length measurement. (download)

Additional File. Effects of Greenfall on Ground-dwelling Arthropods in a Subtropical Forest. (download)