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Litter Moisture Content as a Determinant of Litter Arthropod Distribution and Abundance during the Dry Season on Barro Colorado Island, Panama[1]

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ABSTRACT

Animals generally are patchy in time and space. The causes of this pattern have been explored in only a few cases. We here present data on the relative amounts of migration and activity by litter arthropods during the dry season in artificially watered vs unmanipulated patches of litter on the forest floor of Barro Colorado Island, Panama. Watering significantly changed the physical environment of the litter. Litter moisture content increased by 37–70 percent (absolute increase 8–16%) and soil moisture content by 16–24 percent (absolute increase 4–8%). More and smaller arthropods were found in wetter patches. This effect was weak or variable in watered patches that had unmanipulated arthropod populations and strong in patches from which we had removed arthropods at the beginning of the experiment. Ant colonies were much more likely to migrate into wetter, "empty" areas, and more individuals were collected in these plots. Overall, more species of ants and more groups of arthropods were found in watered, "empty" plots. We thus demonstrate that at least part of the variance in plot-to-plot abundance of litter arthropods is related to litter moisture content. This may have strong effects on the community structure of litter arthropods.

PATCHY SPECIES DISTRIBUTIONS are a common subject of biological investigations (review in Wiens 1976). Many species or groups are patchily distributed, often with no obvious biological explanation (Hairston and Byers 1954, Lloyd 1967). Litter and soil arthropods have been used as examples of this phenomenon (*e.g.,* Macfadyen 1952, Lloyd 1963, Usher 1975). Soil or litter moisture content, insolation, or other abiotic factors frequently are suggested to be important in the formation of uneven distributions among sites (Usher 1970, 1975), but there have been only scattered experimental approaches to this question (Lloyd 1963, Gill 1969, Lussenhop 1976, Vandermeer *et al.* 1980, Whitford *et al.* 1981).

We here present experimental data on arthropod abundance in leaf litter under a tropical semideciduous forest. Using 30 months of data, we previously suggested that the length of the rainy season and the distribution of rain showers in the dry season strongly affect litter arthropods (Levings and Windsor 1982). More litter arthropods were collected (1) when there was a short wet season with low late-wet-season rainfall and (2) when the dry season was punctuated with frequent, small rainshowers. Litter moisture content is more variable in the dry season than the wet season (Levings and Windsor 1982); wetter areas of litter are common on the forest floor during the dry season (pers. obs.). Small areas of moist litter may provide refuges from locally dry conditions for desiccation-intolerant species, permit continued reproduction or foraging activity, or be necessary for successful aestivation.

We report results from an experiment designed to test the effects of variation in litter moisture content during the dry season. Using a combination of removal of the resident arthropods and artificial watering, we examined the pattern of immigration into wetter and into drier "empty" patches of litter. If wetter areas are more attractive to litter invertebrates, then more arthropods should be found in watered than unwatered plots. Similar plots that did not have their resident arthropods removed, but were left undisturbed or were watered, tested for the effects of increased moisture availability on areas that still had a resident arthropod fauna. Differences in resident populations could be the result of three main processes: immigration and emigration, *in situ* reproduction, and increased life or activity span of resident arthropods. These treatments are not directly comparable, because the process of removing the animals (Berlese extraction) undoubtedly changes the chemical or mechanical quality of the litter. However, the direction of changes in the two treatments should be similar if water availability is a major contributor to dry season fluctuations of litter arthropod populations.

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METHODS

We performed our study on Barro Colorado Island, Republic of Panama. This island has been extensively described by many workers, most recently by Leigh *et al.* (1982). The major soil type is described as Frijoles clay (Bennett 1929). The forest is classified as tropical moist forest in the Holdridge life zone system (Holdridge *et al.* 1971) and has a distinctly seasonal pattern of rainfall. The dry season usually extends from December until April, although it may begin any time after November 15 and end any time after March 15 (Rand and Rand 1982). Annual rainfall averages 265 cm/yr (Panama Canal Commission formerly Panama Canal Company rainfall records).

In February 1982, plots of leaf litter, each 0.25 m^2, were haphazardly chosen and flagged on the forest floor. All plots were located within 100 m of each other and were under the forest canopy. Plots were randomly assigned to four treatments: (1) undisturbed control; (2) watered only; (3) arthropods extracted and litter returned; and (4) arthropods extracted, litter returned, and watered. These treatments were designed to contrast the effects of litter moisture content on (1) arthropod numbers in wetter or drier patches of otherwise undisturbed litter (treatments 1 and 2) and (2) movement into wetter or drier "empty" patches of litter (treatments 3 and 4).

Initial samples (removal of arthropods from treatments 3 and 4 using Berlese funnels) were taken from 15–24 February 1982. After Berlese extraction, the dried litter from each treatment plot was kept in a plastic bag for return to its original position on the forest floor. Five replicates of treatments 3 and 4 were sampled every other day during this period. The litter was returned to the forest floor and watering was begun for five sets of the four treatments ($N = 20$ plots on each date) on 24 February, 26 February, 1 March, and 3 March 1982 ($N = 80$ plots total, in four sets of 20).

As much as possible, watering simulated rainfall. Three times weekly, 6.25 liter of water was sprinkled on each watered treatment (treatments 2 and 4) from a large watering can. This totaled the amount of rain (*ca* 35 cm) that falls in an average wet season month (E. Leigh pers. comm.). Care was taken to minimize runoff, but some variability in the amount of water that was actually applied was inevitable. The experiments were run for 31 days from the date of first watering. The five sets of four treatments ($N = 20$ plots of litter) begun 31 days earlier were sampled on 27 March, 29 March, 1 April, and 3 April 1982 ($N = 80$ plots total, 20 replicates of each treatment). Watering continued in unsampled plots until all plots were collected.

To assess differences in moisture availability among treatments, soil samples (top 5 cm) were taken in five sets of treatments 19 days after the beginning of watering. All treatments 1 and 2 were sampled for soil moisture content when they were collected. Soil samples were dried at 105°C, and moisture content was measured as weight loss divided by initial weight.

All Berlese samples were 0.25 m^2 areas of leaf litter. Samples were collected using a frame to delineate the area, placed in plastic bags, and returned to the laboratory. All litter was removed down to the ground layer. Litter samples were weighed and then placed under lights in the Berlese funnels for 24 hours. As the litter heated up, arthropods abandoned it and fell into dilute alcohol. Arthropod samples were removed after 24 hours, cleaned, and stored in 70 percent alcohol until they were sorted. Litter was dried for 24 hours after the arthropod samples were removed (48 hours total, maximum temperature 35°C) and reweighed to determine dry weight.

Arthropods were sorted into size classes and broad taxonomic categories. Size classes were: (1) 0.5–1.49 mm, (2) 1.5–2.49 mm, (3) 2.5–3.49 mm, (4) 3.5–5.49 mm, (5) 5.5–7.49 mm, (6) 7.5–11.49 mm, (7) 11.5–17.49 mm, (8) 17.5–23.49 mm, (9) 23.5–31.49 mm, and (10) over 31.5 mm. Spiders and harvestmen, pseudoscorpions, scorpions, centipedes, and millipedes were sorted to class. Most other groups were sorted to order. All holometabolous larvae were lumped into a single group. Hemimetabolous nymphs were placed with adults of the same order. Ants were sorted to species. The number of ant nests present was estimated by counting a species as nesting in a sample if reproductives or brood of that species were collected in the sample. A species was counted only once, even if several dealate females were collected. This is a conservative estimate of the number of nests collected. Collembolans and mites were counted, but these densities are certainly underestimates. Many are not mobile enough to move out of our funnels; previously we had estimated that only about 5–10 percent are extracted (pers. obs.). We present the counts of collembolans and mites as estimates of relative activity, not accurate estimates of abundance.

As is inevitable in any attempt to manipulate a complex group of organisms, our methods have some drawbacks. First, because quadrat size was fixed at 0.25 m^2, some groups may be inaccurately sampled. This may have affected our sampling of large animals like centipedes, which are always relatively rare (Williams 1941, Levings and Windsor 1982). Second, watering changes both the moisture content and the physical state of the litter. Watered quadrats probably are cooler and may therefore be more attractive or suitable than dry ones. However, this would also be true of naturally wet patches. Compaction due to watering may have reduced the available habitat volume in the litter. We would expect increased compaction of the litter to reduce litter arthropod populations. Any increases due to watering would occur despite this factor. Third, lack of species-level separation in all

groups except ants may obscure some results. Unfortunately, lower-level separation was not feasible. Finally, our funnels were relatively inefficient and can be used only to compare relative catches among treatments. Sampling is a continuing problem in litter arthropod work (*e.g.,* Macfadyen 1962), and some bias appears impossible to avoid.

Because the distribution of litter arthropods among samples is highly non-normal (Levings and Windsor 1982), non-parametric statistics were used in the analyses. Appropriate corrections for ties were always applied. Litter dry weight and litter moisture content data met the assumptions of the analysis of variance; parametric statistics were used for these data.

RESULTS

PHYSICAL VARIABLES.—Litter dry weight and litter percent moisture did not differ in the initial samples of treatments 3 and 4 (t-tests, litter dry weight, litter percent moisture, $N = 20$, each comparison, $P > 0.3$, both tests). Mean dry weight ($\pm$ standard deviation) of litter at the start of the experiment was 110 $\pm$ 30.3 g in treatment 3 and 102.5 $\pm$ 17.2 g in treatment 4. Litter percent moisture averaged 26 percent $\pm$ 8 percent and 28 percent $\pm$ 7 percent, respectively, in treatments 3 and 4.

After 19 days, soil moisture content was significantly higher in the watered replicates sampled (t-test, $P < 0.05$); the absolute difference was about 3 percent (watered quadrats, mean = 35% $\pm$ 3%, control quadrats, mean = 32% $\pm$ 2%, $N = 5$, each sample).

In the final sampling there were no differences among treatments in litter dry weight (one-factor ANOVA, $f_{3,76} = 1.67$, n.s.). Within the pairs of treatments (1 and 2, 3 and 4) there were also no differences ($N = 20$ each comparison, t-tests, $P > 0.1$, both tests). Litter dry weight increased during the course of the experiment because of dry-season litterfall. Final treatment means ranged between 179.8 $\pm$ 38.2 and 212 $\pm$ 51.4 g. The average increase was about 85 g per sample.

Watering produced significant increases in litter percent moisture at all final sample dates ($P < 0.05$ or better, t-tests on litter percent moisture, four sample dates, $N = 10$ watered, 10 unwatered quadrats sampled each date). The absolute difference between treatments varied from 8–16 percent, depending upon rainfall. Watered quadrats averaged 30–37 percent litter moisture content, while unwatered quadrats ranged from 15–25 percent. Soil moisture content increased 3–8 percent in watered quadrats, but the differences were only significant on two sample dates, 29 March and 1 April 1982. In experimental quadrats, the average moisture content stayed near 34 percent; unwatered quadrats averaged between 28 and 30 percent moisture.

Although we attempted to increase litter and soil moisture content to wet-season levels, watering only increased litter moisture content somewhat. Average wet-season litter moisture content is 45–60 percent (Levings and Windsor 1982); only a few sampled quadrats were ever found in this range. However, artificially watered plots are about as moist as the wettest plots collected in random samples from the dry season (Levings and Windsor, unpubl. data). The same pattern was found in soil moisture content. Watering increased soil moisture content by only five percentage points; during the wet season, soil moisture content is five to ten percentage points higher than the values observed in watered quadrats.

ARTHROPOD DENSITY AND SIZE STRUCTURE.—Results for treatments 1 and 2 (unmanipulated litter, unwatered and watered) are presented in Table 1a. More psocids and crickets were collected in unwatered control quadrats than in watered quadrats. More collembolans were collected in watered quadrats. Because so many psocids were collected in the control quadrats (median density = 46/sample), more arthropods were collected in the control plots than the experimentals. This effect is accentuated when all arthropods except ants are considered. Overall, the same numbers of groups of arthropods were collected in all treatments and we found differences in only 5 of 23 comparisons.

There were no statistically significant differences in the number of ants, estimated number of nests, or number of species collected (Table 1a). Median size of ants was similar in both treatments (treatment 1, 2.0 mm vs treatment 2, 1.75 mm, Mann-Whitney U test, $P > 0.3$).

For some groups, treatments 1 and 2 differed in the size structure of arthropods collected. The following groups were abundant enough to test and had a 3 mm or greater size range: beetles, hemipterans, holometabolous larvae, isopods, millipedes, pseudoscorpions, spiders, and harvestmen. Smaller individuals were collected in the watered quadrats for beetles, hemipterans, and isopods (Mann-Whitney U test, $P < 0.05$ or smaller, all tests). Large (>11 mm), julid millipedes were abundant in the watered treatment (7 vs 1 collected), but so few millipedes were collected in these treatments (17 vs 13) that any comparison is obscured. There were no size differences between treatments in the pseudoscorpions, spiders, and larvae. When the size distribution of all arthropods collected was examined, significantly smaller arthropods were collected in the control quadrats (Mann-Whitney U test, $P < 0.01$). This is because large numbers of small (<2 mm) psocids were collected.

Many groups differed in density in comparisons using previously "empty" treatments 3 and 4 (arthropods removed, unwatered and watered, Table 1b). The direction of these differences varied among groups. Watered quadrats contained more of three major decomposer groups:

TABLE 1. *Number of individuals collected for major arthropod groups: Mann-Whitney* U *tests.*[a]

Group	A. Unmanipulated litter, watered and unwatered						B. Manipulated litter (Berlese extraction), watered and unwatered					
	Treatment 1 unwatered		Treatment 2 watered		Probability	Direction of change	Treatment 3 unwatered		Treatment 4 watered		Probability	Direction of change
	Median	(Range)	Median	(Range)			Median	(Range)	Median	(Range)		
Isopoda	1.0	(0–5)	1.0	(0–12)	n.s.	0	1.0	(0–6)	3.0	(0–10)	<0.025	+
Amphipoda	0	(0–1)	0	(0–1)	n.s.	0	0	(0–3)	0	(0–4)	n.s.	0
Diplopoda	0	(0–6)	0.5	(0–5)	n.s.	0	0	(0–1)	1.0	(0–11)	<0.001	+
Larvae[b]	6.5	(0–22)	7.0	(0–14)	n.s.	0	6.0	(0–56)	6.5	(2–77)	n.s.	0
Psocoptera	46.0	(4–341)	17.5	(1–58)	<0.01	−	49.5	(17–160)	17.5	(7–55)	<0.001	−
Thysanoptera	15.5	(0–74)	15.5	(1–42)	n.s.	0	14.0	(0–57)	9.5	(3–46)	n.s.	0
Blattaria	0	(0–2)	0	(0–3)	n.s.	0	0	(0–2)	0	(0–1)	n.s.	0
Gryllidae	1.0	(0–5)	0	(0–4)	<0.05	−	2.0	(0–8)	0	(0–4)	<0.025	−
Hemiptera	1.5	(0–19)	2.0	(0–7)	n.s.	0	2.0	(0–8)	1.0	(0–5)	<0.05	−
Homoptera	0	(0–5)	0	(0–3)	n.s.	0	0	(0–2)	1.0	(0–5)	<0.025	+
Coleoptera	3.5	(0–12)	4.5	(0–25)	n.s.	0	2.0	(0–10)	5.0	(1–23)	<0.01	+
Spiders[c]	24.0	(0–59)	18.0	(3–47)	n.s.	0	30.0	(10–77)	18.0	(5–51)	<0.025	−
Pseudoscorpionida	1.0	(0–23)	1.0	(0–8)	n.s.	0	2.0	(0–6)	3.0	(0–15)	n.s.	0
Chilopoda	0	(0–2)	0	(0–1)	n.s.	0	0	(0–1)	0	(0–3)	n.s.	0
Formicidae												
Number of individuals	28.5	(4–316)	42.5	(6–137)	n.s.	0	20.5	(2–271)	69.5	(6–463)	<0.05	+
Number of species	4.0	(2–12)	5.0	(2–10)	n.s.	0	5.0	(2–11)	7.0	(3–12)	<0.05	+
Number of nests	0	(0–2)	0.5	(0–3)	n.s.	0	0	(0–2)	1.0	(0–3)	<0.05	+
Median size	2.0 mm	(1–3)	1.75 mm	(1–2)	n.s.	0	2.0 mm	(1–3)	1.0 mm	(1–3)	<0.025	−
All arthropods[d]	158.0	(54–582)	142.0	(23–216)	<0.05	−	181.5	(86–438)	159.5	(69–534)	n.s.	0
Non-ant arthropods[d]	126.5	(10–441)	74.0	(8–131)	<0.001	−	133.0	(55–273)	76.5	(58–171)	<0.001	−
Collembola	33.0	(25–150)	73.0	(11–150)	<0.001	+	70.5	(5–230)	95.5	(25–350)	<0.025	+
Acarina	100.0	(15–450)	100.5	(25–250)	n.s.	0	123.0	(35–450)	88.0	(40–275)	n.s.	0
Number of groups[d]	11.0	(8–14)	11.5	(4–14)	n.s.	0	10.5	(5–15)	12.0	(9–15)	<0.05	+

[a] Comparisons corrected for ties.
[b] Larvae = all holometabolous larvae.
[c] Spiders = all Araneae and Opiliones.
[d] Category does not include collembolans or mites.

collembolans, isopods, and millipedes. Total number of macroarthropod decomposers (amphipods, isopods, and millipedes) was significantly greater in watered quadrats (median treatment 4, 4.0, range 0–20, vs treatment 3, 1.0, 0–7, $P < 0.01$, Mann-Whitney U test). We also found more beetles and homopterans in watered than in dry quadrats. Overall, more groups of arthropods were collected in watered quadrats ($P < 0.05$). Unwatered quadrats had more psocids, crickets, hemipterans, and spiders. There were no differences in the numbers of amphipods, holometabolous larvae, thrips, roaches, pseudoscorpions, centipedes or mites.

More ants migrated into empty, watered quadrats than into unwatered quadrats. Median density, numbers of nests, and numbers of species collected all were higher in watered quadrats (Table 1b, $P < 0.05$ or smaller, all comparisons). On average, ants collected in treatment 4 were also smaller: median size was 1 mm in watered treatments and 2 mm in unwatered treatments (Mann-Whitney U test, $P < 0.025$).

Smaller animals were found in watered treatment plots. Size differences were significant for the ants (see above), beetles, larvae, and pseudoscorpions (Mann-Whitney U test, $P < 0.05$ or smaller, all tests), but not for hemipterans, isopods, and spiders. Millipedes followed the same pattern as treatments 1 and 2, but differences in overall density were much greater, precluding any comparison of sizes (treatment 3, $N = 3$, treatment 4, $N = 37$).

The pattern of differences between the two sets of treatments was similar, although many of the comparisons in treatments 1 and 2 were not significant (Table 1). Collembolans were significantly more abundant in both sets of watered quadrats (numbers 2 and 4). Although the differences between numbers of isopods, millipedes, and beetles were not significant in treatments 1 and 2, more of each group were collected in watered quadrats ($N = 27$, 45 isopods, $N = 72$, 113 beetles, $N = 13$, 17 millipedes in treatments 1 and 2, respectively); corresponding differences were significant in treatments 3 and 4. The same pattern holds for all the comparisons concerning ants. More psocids and crickets were collected in unwatered quadrats in both treatment sets. Spiders, which were significantly more common in the unwatered, empty treatment, tended to be more common, although not significantly so, in the treatment 1 control. In no case did the direction of the difference between treatments differ between treatment pairs.

DISCUSSION

Litter moisture content clearly affects the distribution of arthropods on the forest floor during the dry season. The pattern of differences among treatments supports the hypothesis that some of the variance in litter arthropod populations can be attributed to litter moisture content. Although litter dry weight (as a measure of habitat volume or availability of resources) undoubtedly also contributes to variation in litter arthropod populations, this factor did not vary among our treatments (see Results). Litter moisture content is positively associated with the abundance of some groups (ants, beetles, collembolans, homopterans, isopods, and millipedes); it is negatively associated with others (psocopterans, crickets, hemipterans, spiders and harvestmen).

Although the apparent interactions between watering and arthropod removal (Table 1) are intriguing, it is not possible to compare directly the treatments used. Removal of arthropods using Berlese funnels undoubtedly changes the litter physically. Despite the general lack of significant changes in treatments 1 and 2, arthropod groups varied in the same direction in both sets of treatments. This strongly implies that such interactions are probable, for several reasons. First, animals established in quadrats may prevent the immigration of new individuals, limiting the effects of experimental watering. Also, differences in the litter as a result of Berlese treatment may have created substantially different physical environments in the two watered treatments, despite their similarity in litter dry weight and moisture content (see Results). Finally, because replicate size was fixed at 20 and variability between plots is always high (Levings and Windsor 1982), only highly significant interactions were seen.

Differences associated with changes in litter moisture content can be related to the biology of the group in some cases. Ants, beetles, isopods, and millipedes all increase strongly in density at the start of the wet season (Willis 1976, Levings and Windsor 1982) and are more common during a "wet" dry season (Levings and Windsor 1982). From qualitative observations, the same appears to be true of collembolans and mites. Ant abundance in the short term is a function of behavioral responses to favorable physical conditions and perhaps to locally abundant prey concentrations (Levings 1983). Collembolans, some mites, isopods, and millipedes are probably detritivores or fungivores (Kevan 1962); increases in litter moisture content probably increase or at least change food availability by increasing fungal growth or litter decomposition rates. Litter moisture content also may be important in preventing desiccation. These groups usually are reported to be adversely affected by dry conditions (Birch and Clark 1954, Macfadyen 1962, Wallwork 1970); wet patches are attractive as expected. No biological generalization can be made about increases in beetle density in watered quadrats; these increases could have been caused by responses to increased prey density, avoidance of desiccation, or other unknown factors.

Psocids are abundant in litter samples only during the dry season (Willis 1976, Levings and Windsor 1982). They are much more abundant in unwatered than in watered quadrats in both sets of treatments (Table 1).

This may be due to the distribution of food resources during the dry season; wetter patches of litter may have an unsuitable microflora. The same may be true for crickets, which are often detritivores (Kuhnelt 1961, Borror and DeLong 1971). There is no obvious reason why spiders and harvestmen should be more common in dry quadrats; watering itself may have disturbed these animals and lowered their density in watered quadrats. However, all samples were taken 2 days after the last watering. This appears to be enough time for so mobile an animal as a spider to move back into a wet patch, if it were preferred. Compaction of the litter from watering may have contributed to this difference, based on some experimental results from the temperate zone (Bultman and Uetz 1982). We have no data on whether prey availability might contribute to this pattern.

The correlation between moisture content and the density of litter arthropods during the dry season has strong community effects. Local areas of high population density surely are attractive to different arthropod groups for different reasons. Increased decomposition rates or the actual physical conditions in wet patches are probably attractive to decomposer groups such as amphipods, isopods, collembolans, some mites, and millipedes. At least some predators may search preferentially in wetter areas; army ants appear to do so on a larger scale (Levings 1983). Animals that eat psocids would do better to search in drier habitats. These kinds of secondary effects may exemplify how physical preferences are coadapted with aspects of the environment that correlate with foraging success. Why search in the dry areas if the food is in the wet ones?

Finally, we stress that population distributions in tropical areas are the result of interactions among many factors. Physical factors, often assumed to be unimportant in the tropics, cannot be excluded as contributors to the observed variance in animal and plant distributions.

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