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Earthworm abundance and species composition in abandoned tropical croplands: comparisons of tree plantations and secondary forests

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Summary. We compared patterns of earthworm abundance and species composition in tree plantations and secondary forests of Puerto Rico. Tree plantations included pine (*Pinus caribaea* Morelet) and mahogany (*Swietenia macrophylla* King) established in the 1930s; 1960s; and 1970s; secondary forests were naturally regenerated in areas adjacent to these plantations. We found that (1) earthworm density and fresh weight in the secondary forests were twice those in either of the tree plantations, and did not differ between the plantations, and (2) the exotic earthworm species, *Pontoscolex corethrurus* Müller, dominated both plantations and the secondary forests, but native earthworm species, *Pontoscolex spiralis* Borges & Moreno, *Estherella montana* Gates, and *E. gatesi* Borges & Moreno, occurred only the secondary forests. Our results suggest that naturally-regenerated secondary forests are preferable to pine and mahogany plantations for maintaining a high level of earthworm density, fresh weight, and native species.

Key words: Luquillo experimental forest, *Pinus caribaea*, *Pontoscolex corethrurus*, Puerto Rico, restoration, *Swietenia macrophylla*

Introduction

Tree planting accelerates the processes of tree invasion and establishment (Myster 1993) in abandoned agricultural fields. While 1.9 billion ha of tropical forest in the world have been converted for agricultural used (Grainger 1988), many of these lands are abandoned after soils are degraded or because of changes in the local economy. Restoring these fields to their original productivity is an important aspect of maintaining tropical biodiversity (Huston 1993) and sustaining food production (Daily 1995). Towards that end, researchers are evaluating different approaches to rehabilitate vegetation in degraded areas (Brown & Lugo 1994) other than simply allowing them to revegetate naturally through secondary succession. One mechanism is to plant tree seedlings of selected species in order to accelerate the revegetation processes (Wadsworth 1983). Tree plantations represent about 1% of total tropical forests worldwide (Lugo 1992).

Because earthworm often dominate the biomass of soil macrofauna in tropical ecosystems, and may have prominent effects on soil properties by influencing biogeochemical processes that are essential for plant growth (Fragoso & Lavelle 1992; Blair et al. 1995), their dynamics may be key to restoration. High earthworm biomass under similar climate and geological features often indicate high potentials of plant productivity (Lavelle 1988). Tree plantations and secondary forests may differ in influencing earthworm abundance and species composition through the alteration of either soil chemical and physical properties such as

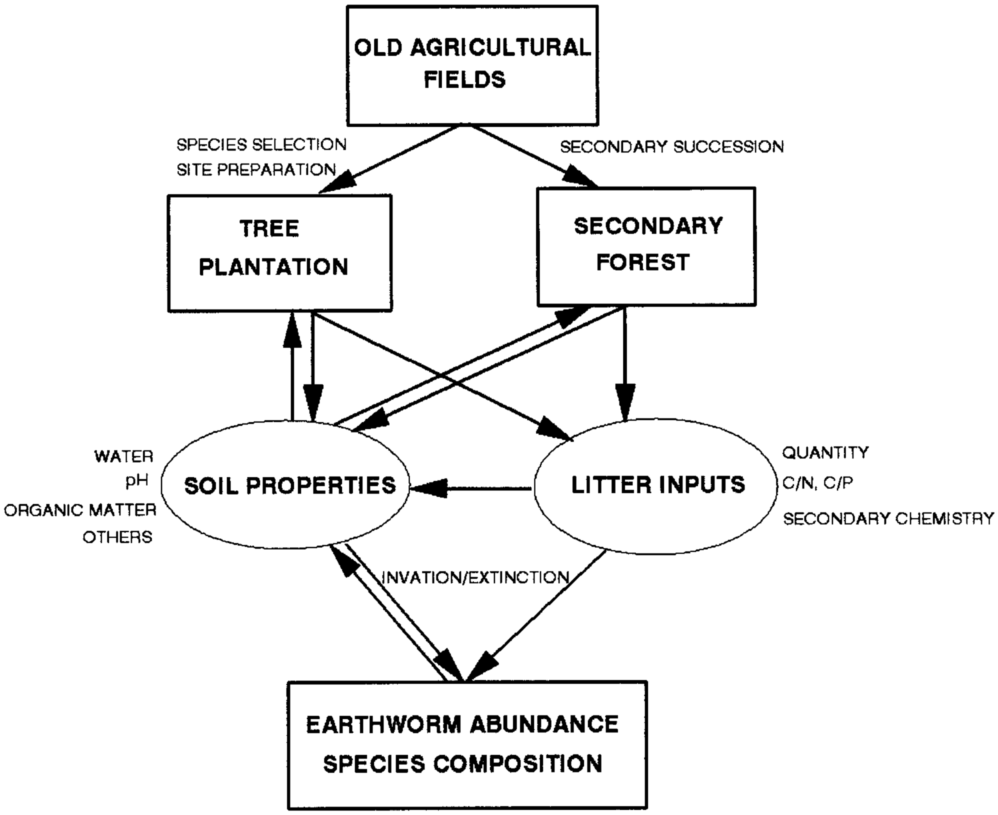

Fig. 1. Conceptual model illustrating the mechanisms by which tree plantations and secondary forests affect earthworm abundance and species composition in abandoned croplands

moisture regime, pH, and soil organic matter levels, or litter inputs (Fig. 1). In addition, litter chemistry such as phenolics content (Bloomfield et al. 1993) may also affect the abundance and species distribution of earthworms (Swift and Anderson 1994).

In Puerto Rico, deforestation occurred extensively between 1830 and 1947 when forest cover declined from 67% to 7% (Birdsey & Weaver 1987) due to agricultural expansion. The development of industry after 1947 released much of those agricultural lands and forest cover increased to 31% by 1989. Small tree plantations were established during the 1930s, 1960s and 1970s in the Luquillo Mountains of Puerto Rico by the U.S.D.A. Forest Service using *Pinus caribaea* Morelet (pine) and *Swietenia macrophylla* King (mahogany). These species are among the most common tree species used in plantations to help recover abandoned agricultural fields throughout the Caribbean and tropical America (Lugo 1992), and they represent about 10% of the world's tropical tree plantation area (Brown et al. 1986). Here we examined the pattern of earthworm density and species composition in pine and mahogany plantations as compared with naturally regenerated secondary forests in Puerto Rico by investigating changes in soil properties (soil water content and pH) and litter quantity and quality (total polyphenolics content).

Materials and Methods

This study was conducted within the subtropical wet forest life zone of the Luquillo Experimental Forest (LEF) of Puerto Rico (Ewel & Whitmore 1973). *Dacryodes excelsa* Vahl is a dominant tree species in a typical mature forest (Zou et al. 1995). Annual precipitation ranges from 2330 to 3920 mm, and the mean annual air temperature is 22.3 °C (Brown et al. 1983). The dominant soils are classified as very-fine, kaolinitic, isohyperthermic Typic Kandiudox, belonging to the Zarzal series (Soil Survey Staff 1995).

Agricultural expansion during the late 19th century and the beginning of this century reached the lower portion of the LEF (Garcia-Montiel & Scatena 1994). Forest was cut and converted to coffee (*Coffea arabica* L.), banana (*Musa* spp.), or yautía (*Xanthosoma* spp.) plantations. However, a tropical storm in 1898 and two hurricanes in 1928 and in 1932 (Scatena & Larsen 1991) struck the Luquillo Mountains and destroyed most of these plantations, leading to their abandonment. In the 1930s, the US Forest Service began to annex these abandoned croplands adjacent to the forest. While allowing secondary succession to proceed under natural conditions in most of these disturbed areas, small tree plantations were established for experimental purposes.

We used three plantations of each tree species (*Pinus caribaea* and *Swietenia macrophylla*) and their adjacent secondary forests, located between 200 m and 600 m elevation in the LEF. Each of the six pairs (plantations/secondary forests) have the same age, and similar topography, soil, and climate conditions. Two pine plantations were established in 1962 and one in 1977 with a 3 × 3 m tree spacing on the abandoned croplands near Cubuy and Guzman, respectively. These lands were cleared by bulldozers before planting pine seedlings. By 1989, the canopy of the pine plantation was mainly a monoculture, but *Casearia sylvestris* Sw., *Didymopanax morototoni* (Aubl.) Decne. & Planch., and *Tabebuia heterophylla* (DC.) Britton were among the native woody species presented in a well developed understory. The average litter production was 7.0 Mg/ha/yr.

Two plantations of *Swietenia macrophylla* were established in 1932 near El Verde Field Station and one in 1963 near Sabana. Tree spacing ranged from irregular to 7.6 × 2.4 m (Lugo 1992). In 1984, the overstory of the plantations were dominated by mahogany, but *Ocotea leucoxylon* (Sw.) Mez., *Tabebuia heterophylla*, and *Myrcia splendens* (Sw.) DC. were also found in the understory. Average litter production was 10.8 Mg/ha/yr.

Secondary forests were naturally regenerated adjacent to the pine and mahogany plantations on the same abandoned lands with similar soil conditions. By 1989, the secondary forests were dominated by *Tabebuia heterophylla*, *Casearia arboria* (L.C. Rich) Urban, *Syzygium jambos* (L.) Alston, and *Manilkara bidentata* (A. DC.) Cehv. Average litter production was 6.15 Mg/ha/yr (Cuevas et al. 1991; Lugo 1992).

All field data were obtained between January and May, 1994. Earthworms were sampled in two plots (0.5 × 0.5 m) randomly located in each plantation or its adjacent secondary forest for a total of 24 plots. Ground litter (leaves and twigs < 2 mm) was collected from each plot and litter biomass was obtained after drying leaves and twigs at 60 °C for at least 72 hrs. Leaves were analyzed for total extractable polyphenolics content using the Folin-Denis reagent (Horowitz 1970, Anderson & Ingram 1989) and were reported as percent tannic acid equivalent (%TAE). Soils beneath the litter were collected by shovel to a depth of 0.25 m and placed onto a cloth sheet. Earthworms were hand sorted and stored in plastic bags in a cooler with ice. Fresh weight of earthworms was recorded after the worms were rinsed with water and dried with paper towels on the same day when they were collected. A small subsample of the soil (0 – 0.25 m) was used for measuring pH and moisture content. Soil water content was calculated for each site by oven drying 10 g of fresh sample at 105 °C for 48 hrs and reported on the oven-dry basis. Soil pH was measured using a paste of 1 : 1 ratio of fresh soil and deionized water. Data was analyzed using ANOVA (SAS 1987) to compare differences among the plantations and the secondary forests. Where significant differences were found, Duncan's multiple range test was employed to compare differences among pine, mahogany and secondary forest. Earthworm density and fresh weight were correlated with soil pH, moisture content, ground litter biomass, and litter polyphenolics content using a simple linear correlation analysis (SAS, 1987).

Results and Discussion

Earthworm density and fresh weight in the secondary forest were twice those in either of the tree plantations and did not differ between pine and mahogany plantations (Table 1). There was a total of five worm species found in all plots (Table 2). Among the two exotic earthworms, the endogeic species *Pontoscolex corethrurus* dominated both plantations and the secondary forest, and the anecic species *Amynthas rodericensis* occurred in the pine plantation and the secondary forest. However, the native and soil-feeding species *Estherella gatesi*, *Estherella montana*, and *Pontoscolex spiralis* were found only in the secondary forest

Table 1. Earthworm density, fresh weight, soil pH and water content, polyphenolics content, and ground litter biomass in tree plantations and secondary forest in Puerto Rico

Treatment	Density (No m^{-2})	Fresh weight ($g\ m^{-2}$)	Soil H_2O (%)	Soil pH	Litter poly-phenolics*	Litter biomass ($g\ m^{-2}$)
Pinus caribaea	91.3 ± 7.7b	30.8 ± 1.8b	52.8 ± 4.6b	4.7 ± 0.1a	0.48 ± 0.02b	1037.3 ± 33.8a
Swietenia macrophylla	106.7 ± 5.7b	29.5 ± 1.4b	50.7 ± 5.8b	5.0 ± 0.1a	1.19 ± 0.48a	554.7 ± 17.5b
Secondary forest	189.3 ± 6.8a	61.4 ± 2.0a	59.7 ± 3.5a	5.1 ± 0.1a	0.86 ± 0.09a	328.8 ± 11.3b

§ Mean ± standard error; common letters within a column indicate no significant difference among treatments Duncan's multi-range test, $\alpha = 0.05$); * Total polyphenolics is given as % tannic acid equivalent

Table 2. Native and exotic earthworms in tree plantations and secondary forest in the Luquillo Experimental Forest of Puerto Rico

Treatment	Native species	Exotic species
Pinus caribaea	None	*Pontoscloex corethrurus* (Muller, 1856) *Amynthas rodericensis* (Grube, 1879)
Swientenia macrophylla	None	*Pontoscolex corethrurus*
Secondary Forest	*Pontoscolex spiralis* (Borges and Moreno, 1990) *Estherella montana* (Gates, 1970) *Estherella gatesi* (Borges and Moreno, 1989)	*Pontoscolex corethrurus* *Amynthas rodericensis*

(Table 2). There were no native earthworms in the tree plantations. Together, pine and mahogany plantations supported two worm species, whereas the secondary forest supported a total of five worm species.

Soil water content ranged between 50 – 60% during the sampling period between January and May 1994, and was significantly higher in the secondary forest than in the tree plantations (Table 1). Soil water content did not differ between pine and mahogany plantations. Soil pH did not differ among the tree plantations and the secondary forest. Total polyphenolics content of ground leaf litter in the mahogany plantation and the secondary forest was significantly higher than that in the pine plantation, but did not differ between mahogany plantation and the secondary forest. Ground litter biomass in the pine plantation was two to three times that in either the mahogany plantation or the secondary forest which did not differ from each other. Earthworm density and fresh weight correlated significantly with soil water content (Table 3). Earthworm fresh weight was significantly and negatively correlated with ground litter biomass. Soil pH and total polyphenolics content of leaf litter did not correlate with either worm density or fresh weight.

Earthworm density in the tree plantations was half that in the paired secondary forest. There were no native earthworm species in tree plantations. Zou and González (in press) studied changes in earthworm abundance and community structure during natural succession from pasture land to secondary forest, and found that native worms occurred only in secondary forest 20 years after the abandonment of pastures. Factors contributing to the differences in worm abundance and species composition between plantations and

Table 3. Correlation coefficients (significance level) between earthworm density and fresh weight with soil pH, soil water content, leaf total polyphenolics content, and litter biomass in plantations of *Pinus caribaea* and *Swietenia macrophylla* and their adjacent secondary forest

Variable	Soil H_2O (%)	Soil pH	Litter polyphenolics (%)	Litter biomass ($g\,m^{-2}$)
Earthworm density	0.40	0.07	0.25	−0.26
(No. m^{-2})	(0.05)	(0.74)	(0.23)	(0.24)
Earthworm fresh	0.49	0.22	0.32	−0.48
weight ($g\,m^{-2}$)	(0.01)	(0.29)	(0.13)	(0.02)

naturally regenerated forest might include differences in soil water content, soil pH, organic matter content, and the quantity and chemistry of litter inputs (Fig. 1). In addition to its effect on soil physical properties, site preparation using bulldozers may bury nutrient rich top soil and course soil erosion, thus reducing surface soil organic matter content and nutrient availability to plants. Tree species selection often alter above- vs. below-ground carbon allocation pattern and the chemistry of litter inputs.

In this study, there were no significant differences in soil pH among the treatments. Lugo (1992) reported that in 1980, soil organic matter content was 88 Mg/ha for the 1977 pine plantation compared with 78 Mg/ha in the paired secondary forest, and was 177 Mg/ha for the 1962 pine plantation as compared with 171 Mg/ha in the paired secondary forest. Soil organic matter content was higher in the 1963 mahogany plantation than its paired secondary forest, but was lower in thw 1932 mahogany plantation than its paired secondary forest, showing an inconsistent pattern. These data suggested that differences in soil pH and soil organic matter content did not play an important role in triggering differences in earthworm abundance and species composition between tree plantations and the secondary forest.

Lugo (1992) showed that in 1983 the pine and mahogany plantations had a similar litterfall rate which is higher than the secondary forest. In our study, ground litter biomass did not differ between mahogany plantation and the secondary forest (Table 1). The secondary forest was not significantly different in total polyphenolics content from the mahogany plantation. Total polyphenolics content of leaf litter did not correlated with either worm density or fresh weight (Table 3). We observed the highest and lowest values of total polyphenolics content in the mahogany and pine plantations, respectively, but the highest earthworm fresh weight and density occurred in the secondary forest. Although both pine and mahogany are exotic trees to Puerto Rico, the species composition in the understory of a 1932 plantation was approaching that of the secondary forest and included many native trees (Lugo 1992). These data suggested that differences in the quantity of above ground organic input, litter total polyphenolics content, and in the composition of dominant tree species did not explain the large differences in earthworm abundance and species composition between plantations and the secondary forest.

Zou (1993) showed that earthworm abundance correlated positively with litterfall nitrogen content in Hawaiian tree plantations. Lugo (1992) demonstrated that in our study sites, total nitrogen input through litterfall did not show a consistent pattern between plantations and the secondary forest, but total phosphorus input was consistently higher in the secondary forest than in the paired plantations. In addition, soil water content was the highest in the secondary forest and significantly correlate with earthworm density and fresh weight. Cuevas et al. (1991) reported that 44% of the total net primary productivity was allocated to below-ground biomass in the secondary forest, whereas 94% was allocated to above-ground biomass in the 1977 pine plantation. Live and dead fine roots in the secondary forest were significantly higher than in the plantations. Microbial biomass in the 1932 mahogany plantation was lower than that in the paired secondary forest (S. Fu et al. 1995, unpub. data). Root and microbial biomass is likely the major food source for endogeic earthworms (Lee 1985). A field experiment demonstrated that microbial respiration rate increased after the addition of phosphorus to soils in mature tabonuco forest (J. Lodge, 1991, unpub. data). Thus, low soil phosphorus availability coupled with low water content and low below-ground root biomass in the plantations are likely the major factors limiting earthworm population in pine and mahogany plantations. Site preparation using bulldozers may also enhance phosphorus limitation effect by exposing phosphorus poor sublayer soils to the surface.

We examined the effects of pine and mahogany plantations on earthworm abundance and species composition in abandoned croplands of Puerto Rico. Our data suggest that the naturally regenerated secondary forest supports a higher level of worm density, fresh weight, and native species than do pine or mahogany plantations. Differences in soil water content, P availability, root and microbial biomass may contributed to the observed difference in worm abundance and species composition between the plantations and the secondary forest. In addition, naturally regenerated forest is preferred by native earthworms. Other tree plantations that differ in carbon allocation pattern, water evapotranspiration potentials, and in litter chemistry may impose different effects on worm abundance and species composition. Therefore, cautions should be paid to make a generalization about the effects that other tree plantations may have on earthworm abundance and species composition.

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References

Anderson, J. M., Ingram, J. S. I. (1989) Tropical Soil Biology and Fertility: A Handbook of Methods. C.A.B. International, Wallingford, UK.

Birdsey, R. A., Weaver, P. L. (1987) Forest Area Trends in Puerto Rico. USDA Forest Service Research Note SO-331. pp. 5. Inst. of Tropical Forestry. Rio Piedras, PR.

Blair, J., Parmelee, R. W., Lavelle, P. (1995) Influences of earthworms on biogeochemistry. In: Hendrix, P. F. (ed) Earthworm ecology and biogeography in North America. Lewis Publishers, Boca Raton, FL, USA.

Bloomfield, J., Vogt, K. A., Vogt, D. J. (1993) Decay rate and substrate quality of fine roots and foliage of two tropical tree species in the Luquillo Experimental Forest, Puerto Rico. Plant Soil **150**, 233–245.

Borges, S., Moreno, A. G. (1989) Nuevas especies del género *Estherella* Gates, 1970 (Oligochaeta: Glossoscolecidae) para Puerto Rico. Boll. Mus. Reg. Sci. nat. Torino **7**, 383–399.

Borges, S., Moreno, A. G. (1990) Nuevas especies y un nuevo subgénero del género *Pontoscolex Schmarda*, 1861 (Oligochaeta: Glossoscolecidae) para Puerto Rico. Boll. Mus. Reg. nat. Torino **8**, 143–157.

Brown, S., Lugo, A. E. (1994) Rehabilitation of tropical lands: a key to sustaining development. Restoration Ecology **2**, 97–111.

Brown, S., Lugo, A. E., Chapman, J. (1986) Biomass of tropical tree plantations and its implications for the global carbon budget. Can. J. For. Res. **16**, 390–394.

Brown, S., Lugo, L., Silander, S., Liegel, L. (1983) Research History and Opportunities in the Luquillo Experimental Forest. Gen. Tech. Rep. SO-44, USDAForest Service, Washington DC, USA.

Cuevas, E., Brown, S., Lugo, A. E. (1991) Above- and below-ground organic matter storage and production in a tropical pine plantation and a paired broadleaf secondary forest. Plant Soil **135**, 257–268.

Daily, G. C. (1995) Restoring value to the world's degraded lands. Science **269**, 350–354.

Ewel, J. J., Whitmore, J. L. (1973) The Ecological Life Zones of Puerto Rico and the U.S. Virgin Islands. Res. Pap. ITF-18, USDA Forest Service, Washington DC, USA.
Fragoso, C., Lavelle, P. (1992) Earthworm communities of tropical rain forests. Soil Biol. Biochem. **24**, 1397 – 1408.
Garcia-Montiel, D., Scatena, F. N. (1994) The effect of human activity on the structure and composition of a tropical forest in Puerto Rico. For. Ecol. Manage. **63**, 57 – 78.
Gates, G. E. (1970) On new species in a new earthworm genus from Puerto Rico. Breviora **356**, 1 – 11.
Grainger, A. (1988) Estimating areas of degraded tropical lands requiring replenishment of forest cover. International Tree Crops Journal **5**, 31 – 61.
Grube. (1879) Phil. Trans. Roy. Soc. London **168**, 554.
Horowitz, W. (1970) Official methods of analysis of the association of official analytical chemists, p. 154. AOAC, Washington, D.C., USA.
Huston, M. (1993) Biological diversity, soils, and economics. Science **262**, 1676 – 1680.
Lavelle, P. (1988) Earthworm activities and the soil systems. Biol. Fertil. Soils **6**, 237 – 251.
Lee, K. (1985) Earthworms: Their Ecology and Relationships with Soils and Land Use. Academic Press, New York, USA.
Lugo, A. E. (1992) Comparison of tropical tree plantations with secondary forests of similar age. Ecol. Monogr. **62**, 1 – 41.
Myster, R. W. 1993. Tree invasion and establishment in oldfields at Hutcheson Memorial Forest. The Botanical Review **59**, 251 – 272.
SAS, Inc. (1987) SAS Guide for Personal Computers, 6th ed. Cary, North Carolina, USA.
Scatena, F. N., Larsen, M. C. (1991) Physical aspects of hurricane Hugo in Puerto Rico. Biotropica **23**, 317 – 323.
Soil Survey Staff. (1995) Order 1 Soil Survey of the Luquillo Long-Term Ecological Research Grid, Puerto Rico. USDA NRCS, Lincoln, NE, USA.
Swift, M. J., Anderson, J. M. (1994) Biodiversity and Ecosystem Function in Agricultural Systems. In: Schulze, E. D. & Mooney, H. A. (eds) Biodiversity and Ecosystem Function. Springer-Verlag, New York, USA.
Wadsworth, F. H. (1983) Production of Usable Wood from Tropical Forests. In: Golley, F. B. (ed) Tropical rain forest ecosystems. Elsevier, Amsterdam, The Netherlands.
Zou, X. (1993) Species effects on earthworm density in tropical tree plantations in Hawaii. Biol. Fertil. Soils **15**, 35 – 38.
Zou, X., Gonzalez, G. (in press) Changes in earthworm density and community structure during secondary succession in abandoned tropical pastures. Soil Biol. Biochem.
Zou, X., Zucca, C. P., Waide, R. B., McDowell, W. H. (1995) Long-term influence of deforestation on tree species composition and litter dynamics of a tropical rain forest in Puerto Rico. For. Ecol. Manage. **78**, 147 – 157.

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Separation of trophic niches by dung beetles (Coleoptera, Scarabaeoidea) in overlapping habitats

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Summary. In heterogeneous landscapes, mammals deposit excrement non-randomly. In pastures, some dung is concentrated over small areas, several hundred square metres for resting places of sheep flocks, $0.5-2$ m^2 for dung-heaps of wild rabbits. Fresh scattered sheep pellets and trampled dung from sheep resting places and from rabbit dung-heaps constitute distinct trophic niches exploited by distinct dung beetle communities. The organization of dung beetle assemblage of winter-deposited sheep pellets (climatic constraints) is very similar to the organization of dung-heaps and sheep resting-place assemblages (edaphic constraints). Each species assemblage corresponds to a nomocenose, an aggregate of organisms living together in a particular habitat with a log-normal or a log-linar distribution of abundance. The juxtaposition of the nomocenoses increases biotic diversity in heterogeneous landscapes.

Key words: Dung beetles, community structure, nomocenose, trophic niche, heterogeneous landscape, Motomura's model

Introduction

Humans have greatly altered habitats through their activities (agriculture, forestry, cultural practices). In Western Europe, habitats have been dissected into many small isolated patches which may be expected to affect biotic diversity adversely (Van Dorp & Opdam 1987). Landscape features influence a wide variety of ecological patterns and processes. Wiens and Milne (1989) demonstrated the role of landscape structure as a modifier of beetle movements or of diffusion in heterogeneous landscape. The vegetation structure also influences the distribution of dung beetles which are generally more abundant in open sites (Lumaret 1983). The vegetation cover acts like a filter that allows the penetration of several ubiquitous but fundamentally open-habitat dung beetle species into forests, at the same time drastically limiting their numbers. Dung beetles attracted by mammal droppings comprise a small number of families, mostly the Aphodiidae and Scarabaeidae which are predominantly dung feeders although not exclusively so. Some saprophagous beetle species can be reared on dung, while some coprophagous species can be reared successfully on humus (Cambefort 1991). Most Scarabaeidae dig tunnels beneath pats, line them with dung and store balls of dung in them. The females lay eggs inside the balls of dung, which serve as a food for the larvae. The adults live on the dung pats for short periods before flying off in search of new pats. Most Aphodiidae species do not bury dung as food store for their progeny but live and breed in the dung pats while they are still on the surface. However, under Mediterranean climatic conditions, several species dig primitive tunnels and larvae develop in the soil beneath dung pellets (Rojewski 1983; Lumaret & Kirk 1991;

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