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Direct and indirect effects of soil structure on the density of an antlion larva in a tropical dry forest

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Abstract. 1. We used structural equation models to discriminate direct and indirect effects of soil structure on the abundance of the antlion *Myrmeleon crudelis*, a neuropteran larva that digs conical pits in soil to capture small arthropods. We proposed that soil structure may modify antlion density indirectly through its influence on tree cover, which in turn directly alters the amount of sun and rain that can reach the forest floor and the amount of litter fall.

2. The proportion of finer soils positively affected antlion density directly, but negatively tree cover. Tree cover positively affected both the amount of leaf litter and antlion density. Leaf litter negatively affected antlion density. The indirect effects of soils varied in strength and sign depending on whether trees are considered shelters against sun and rain, or leaf litter sources. The relative importance of these effects might also vary between years and seasons.

3. Antlions may select patches of finer soils not only because they are easy substrates in which to build pits, but also for their indirect benefit as sites with low leaf litter, illustrating how indirect interactions may affect the local abundance of semi-sedentary insects.

Key words. Abiotic factors, Costa Rica, habitat selection, indirect interactions, *Myrmeleon crudelis*, path analysis, structural equation model.

Introduction

Our understanding of how biotic and abiotic variables affect population structure is largely based on studies of direct effects, probably because they are often straightforward and easy to measure. Using this approach, ecologists have shown that predation and climate have important effects on population organisation (Price, 1997). However, direct effects represent an incomplete picture of the mechanisms that really structure the organization of a given population. First, abiotic and biotic variables may interact, affecting populations through indirect effects. For example, litter nutrients and changes in rainfall may influence invertebrate litter fauna directly, by regulating food availability and survival, or indirectly through their interaction with parasitoids and predatory arthropods (Lensing & Wise, 2006; Classen *et al.*, 2007; McGlynn *et al.*, 2007). Climate changes may influence the population of insect herbivores directly by altering their survival, reproduction and dispersal and indirectly by altering the susceptibility and resistance of their host plants to insect attack (Dale, 2001). Second, direct and indirect effects with opposite polarities may result in zero net effect and thus be indistinguishable in correlational studies (Dyer & Letorneau, 1999). For example, the negative impact of a predator on a target prey may be compensated with a release in competitive pressure as a consequence of predation on other prey that compete with the first (Holt, 1977). Therefore, it is important to understand the identity and the relative importance of indirect interactions to elucidate mechanisms that structure populations (Wootton, 1994).

Insects with limited mobility are ideal subjects to study the importance of indirect effects of abiotic factors on animal abundance. As semi-sedentary animals rarely move once

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established, the identification of the local conditions that mainly affect their abundance is easier than in mobile animals. Antlion larvae (Neuroptera: Myrmeliontidae), the focus of the present study, are sit-and-wait predators that dig conical pits in loose soil to capture small arthropods (usually ants) that fall into the pit. Both abiotic and biotic factors may affect the fitness of such organisms, and therefore patterns of variation in their local abundance (Gotelli, 1993; Crowley & Linton, 1999). However, several studies suggest that abiotic factors are relatively more important than biotic factors (Scharf & Ovadia, 2006). For example, while local abundance of antlion pits is not correlated with prey availability (Gotelli, 1993, 1996, 1997; Crowley & Linton, 1999), abiotic factors such as soil moisture, leaf litter, soil temperature, rainfall, and soil structure often restrict the habitat available to antlions (McClure, 1976; Simberloff *et al.*, 1978; Boake *et al.*, 1984; Marsh, 1987; Lucas, 1989; Gotelli, 1993; Gatti & Farji-Brener, 2002; Farji-Brener, 2003).

Abiotic factors can directly affect antlion abundance in different ways. For example, high soil surface temperature often kills antlions by desiccation (but see Matsura & Murao, 1994); larvae that remain under direct sun can die in a few minutes (Marsh, 1987; Lucas, 1989; Gotelli, 1993; Gatti & Farji-Brener, 2003). Strong rainfall can directly destroy pits. Falling leaves and twigs may also damage pits and once they land on the forest floor, they might cover pits and reduce the probability of prey capture (Griffiths, 1980; Gatti & Farji-Brener, 2003). However, soil consistency is probably one of the most important abiotic factors that influence the abundance of this sit-and-wait predator (Scharf & Ovadia, 2006). Antlions prefer soils with a high proportion of fine-grained particles, for several reasons: the larvae require less time to build the pit, and construct larger and deeper pits that increase prey capture (Lucas, 1985; Botz *et al.*, 2003; Farji-Brener, 2003; Devetak *et al.*, 2005). Consequently, antlions are often less abundant in areas with high soil surface temperature, soils exposed to rainfall, sites with high abundance of leaf-litter, and coarse-grained soils (McClure, 1976; Lucas, 1982; Gotelli, 1993; Crowley & Linton, 1999; Arnett & Gotelli, 2001; Lomascolo & Farji-Brener, 2001; Farji-Brener, 2003).

In addition to these direct effects, soil structure (i.e. soil particle size) may also affect antlion density in more subtle ways, for example through indirect effects mediated by their potential influence on plants. The physical characteristics of soils affect seedling establishment, plant growth and plant abundance (Bazzaz, 1996). Plant abundance and/or cover, in turn, may influence (i) the temperature of the soil surface directly by creating shade and (ii) the amount of leaf litter and rain that reach the forest floor (Fig. 1). As discussed above, soil surface temperature, rainfall and leaf litter are factors that potentially affect antlion density. However, to our knowledge no studies have ever considered the indirect consequences of soil structure on antlion populations through its influence on plants. In this study, we discriminated direct and indirect effects of soil structure on the abundance of the antlion larva *Myrmeleon crudelis* in a tropical dry forest of Costa Rica. To do this, we sampled soil particle size, tree cover and the amount of leaf litter in plots that differed in antlion abundance and used structural equation modelling (hereafter SEM) to identify direct and indirect effects of soil particle size on the abundance of *M. crudelis*.

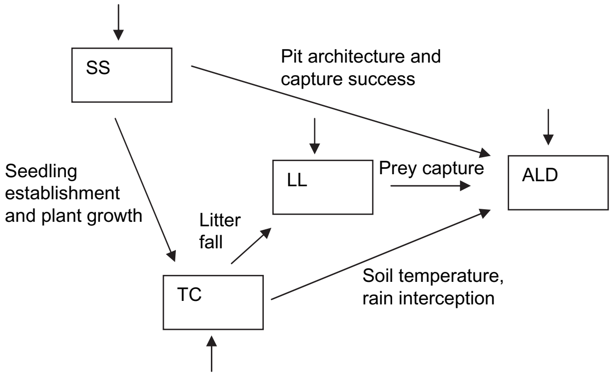


Fig. 1. Causal model used to determine direct and indirect effects of soil structure (SS), tree cover (TC) and leaf litter (LL) on antlion density (ALD). One-headed arrows represent directional effects. Unexplained variability is indicated with vertical arrows. Biological effects associated with each path are included.

Methods

Ant-lion natural history, study site and methods

Adult antlions are nocturnal, short-lived and weak flying insects. After mating, females lay many eggs in the soil from which larvae emerge. Larvae are sessile predators; they dig a conical pit in dry, loose substrate protected from wind and rain and feed on prey falling into these traps. The duration of the larval stage is highly variable, requiring at least 1–3 years to mature (Gotelli, 1993). In tropical dry forest of Costa Rica, the most abundant antlion species, *M. crudelis*, is restricted to bare soils along forest trails, at the bases of large trees, below overhanging rocks, and underneath logs (McClure, 1976).

This study was carried out in February 2007 during the dry season in Palo Verde National Park (10°N, 85′W), a tropical dry forest located in the Guanacaste Province, Costa Rica. Characteristic trees include deciduous species such as *Bursera simaruba*, *Pithecellobium saman*, *Guazuma ulmifolia*, *Spondias mombin*, and large areas with the understory ant-plant *Acacia collinsii*. Mean annual rainfall is 1500–2000 mm and highly seasonal. Almost no rain falls from November to May, when many plants drop their leaves. Mean annual temperature is 27 °C but soil surface temperature may reach up to 60 °C at midday.

To determine direct and indirect effects of soil structure on the abundance of *M. crudelis*, we randomly established 18 plots of 50 × 50 cm along three forest trails (La Roca, La Venada and Mapache) as well as around the field biological station of Palo Verde. Because our goal was to understand the variation in antlion density, not the factors that determine the absence or presence of pits, the locations of the plots were areas that were occupied by at least one antlion pit; thus areas without antlions were not considered. The distance between plots was >10 m. In each plot we measured soil structure (SS), tree cover (TC), the amount of leaf litter (LL) and the number of antlion larvae pit traps (ALD). Soil structure was classified according to its percentage of soil particles with different sizes (<2 mm to >6 mm). To estimate the per cent of fine soil particles we followed Gotelli's (1993) methodology (see also Farji-Brener, 2003). In each plot, we collected three soil samples of ≈ 100 g from the upper 5 cm of the soil. Soil samples were air dried for 2 days, and then subdivided according to grain size using a series of sieves (<2 mm, 2–6 mm, and >6 mm). Sieved fractions were individually weighed, and their weights were converted to percentages of the total sample. In analyses of preferences, we only employed the per cent of particles <2 mm, because earlier studies demonstrated that *M. crudelis* strongly prefers this soil particle size to build pits (Lomascolo & Farji-Brener, 2001; Farji-Brener, 2003). To estimate the tree cover, we used a concave spherical densitometer. We visually divided each plot into four quadrants to make four densiometer readings, one in each quadrant. We averaged the four cover values to estimate an overall estimation of tree cover for each plot. To estimate the amount of leaf litter, we subdivided the 50×50 cm plot into 25 cells of 10×10 cm and counted the number of subdivisions covered by leaf litter. This number was multiplied by four to estimate the proportion of leaf litter per plot. Finally, we counted the total number of occupied pits per plot as an estimation of antlion density (larvae/0.25 m^2). Pits were also sought beneath leaf litter; larval presence was tested in each pit measured. Larvae outside pits were never observed.

Statistical analysis

The total co-variation between two variables is usually estimated by their correlation value. However, the correlation between two variables represents a net effect, which often is a composite measure of direct and indirect effects (Legendre & Legendre, 2004). To identify these components of the net effect between soil structure and the density of *M. crudelis*, we used structural equation models (SEM; Shipley, 2000). This methodology was originally developed as path analysis, as a way to partition the variation from observational data into causal and non-causal components (Mitchell, 2001). We constructed a general model in which we could partition the net effect of soil structure on antlion density into direct and indirect effects. We proposed two indirect effects. Soil structure may affect antlion abundance indirectly through their effect on tree cover, which in turn influences antlion density (i) directly, through their effect on soil surface temperature and on the level of rain interception; and (ii) indirectly, through their relationship with the quantity of leaf litter that falls to the forest floor (Fig. 1). The fit of the model with the data was evaluated via SEM using χ^2 and associated probabilities (higher *P*-values indicated better fits; Shipley, 2000), and pathways were evaluated by their *t*-values and associated probabilities. Path coefficients were computed using standardized variables (i.e. all variables were standardized to have unit variance). We calculated total co-variation using Pearson's correlation coefficients (*r*), and estimated non-causal co-variation as *r* values minus the sum of direct and indirect effects (Legendre & Legendre, 2004). The values of indirect effects were obtained by multiplying the respective path coefficients from the pathway proposed (Fig. 1). For example, the indirect effect of SS on ALD through TC was estimated as the product of the SS-TC and the TC-ALD path coefficients.

Results

The plots sampled showed great variation in all the variables measured. The number of *M. crudelis* larvae varied between 1–9/0.25 m^2, the proportion of fine-grained particles varied between 10–65%, tree cover varied between 1–71% and the quantity of leaf litter varied between 0–76%. The proposed model fits very well with the data ($\chi^2 = 0.01$, d.f. $= 1$, $P = 0.90$, Fig. 2), supporting our hypothesised causal scheme to explain the effect of soil structure on antlion density (Fig. 1). The model explained the variation in density of *M. crudelis* well (70%) but only a small proportion of the variation in tree cover and the amount of leaf litter (14–28%). The direct effect of soil structure on antlion density was positive and significant (0.44), but the sign and strength of their indirect effects varied according the proposed paths. Soil structure negatively affected tree cover (–0.53) and tree cover positively affected both the amount of leaf litter (0.37) and antlion density (0.22). On the other hand, leaf litter negatively affected the density of *M. crudelis* (–0.75). Therefore, the indirect effect of soil structure on antlion density through changes on

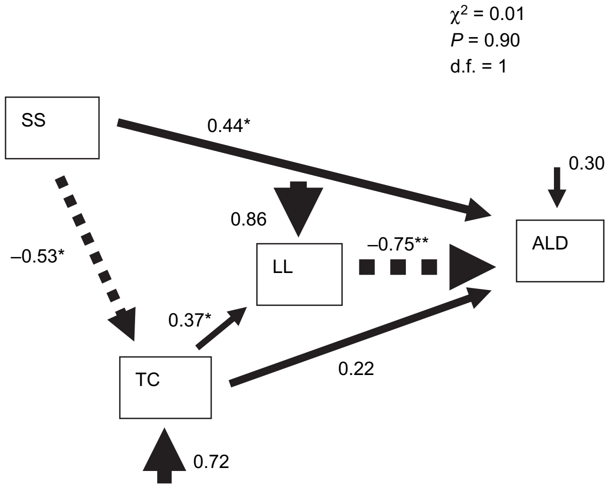
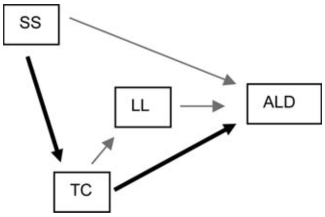
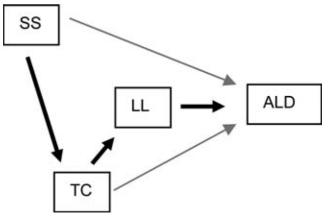


Fig. 2. Path analysis of the causal relationship between soil structure (SS), tree cover (TC) and leaf litter (LL) on antlion density (ALD). One-headed arrows represent direct causal effects. For each effect path, coefficients are given and are also represented by arrow line thickness. Continuous lines indicate positive effects; dashes lines indicate negative effects. Significance of the path coefficients is indicated as follows: * $P < 0.05$, ** $P < 0.01$. Unexplained variability is indicated with vertical arrows. The adequacy of models was evaluated based on model χ^2 and associated *P*-values (a higher *P*-value, means a better fit of the model with the data).

tree cover varied in strength and sign depending on the path examined (Fig. 2). Soil structure negatively affected antlion density through its effect on tree cover (–0.12) but positively when the effect of tree cover on leaf litter was incorporated (0.15) (Table 1). On the other hand, the net effects of soil structure, tree cover, and leaf litter on antlion density (total co-variation estimated using Pearson's coefficients) were positive ($r = 0.48$), and negative ($r = -0.29$ and –0.75, respectively). Despite the fact that the direct effect of soil structure (0.45) appeared to be the strongest contribution to the net effect on antlion density ($r = 0.48$), indirect effects were also important (relative importance of 0.6). The contribution of indirect effects on the net effect was hidden because they showed similar values but opposite signs (–0.12 and 0.15, Table 1). The sum of direct and indirect effects was very similar to the total co-variation values between soil structure and antlion density, suggesting the absence of non-causal co-variation effects (Table 1).

Table 1. Direct and indirect effects of soil structure (SS) on antlion density (ALD).

	Bivariate relationship
	SS-ALD
Total co-variation (r)	0.48
Direct effect	0.45
Indirect effects of SS on ALD	
a. Via TC  	–0.12
b. Via TC and LL  	0.15
Total effect (direct + indirect)	0.48
Non-causal co-variation	0
Indirect/direct effects	0.60

TC, tree cover; LL, leaf litter (see Fig. 1). Total co-variation between SS and ALD was estimated by correlation coefficients (r). Direct effects and indirect effects were estimated using the path values of the SEM (see text). Non-causal co-variation was estimated as r–(direct + indirect effects). The relative importance of indirect effects was estimated as (indirect/direct effects). Values larger than one suggest relatively more importance of indirect effects, similar to one represent similar relative importance, and smaller than one relatively more importance of direct effects. Diagrams of indirect effects were added to increase clarity; black arrows indicate the indirect pathway analysed in each case.

Discussion

Previous studies regarding the influence of soil structure on antlion larvae have dealt with its direct effects on pit construction and prey capture success (reviewed in Scharf & Ovadia, 2006). These studies, along with the results presented here, have shown that the proportion of fine-grained particles has important effects on larval density because in finer soils, pits are easier to build and more effective in capturing prey (Lucas, 1982; Botz *et al.*, 2003; Farji-Brener, 2003). Our study demonstrates that soil structure can also have subtler indirect impacts on antlion larvae when its effect on plants is incorporated (Fig. 1).

We found that the proportion of fine-grained soil particles was negatively associated with tree cover. Changes in soil structure may affect seedling establishment and plant growth, because they modify the level of soil aeration and therefore oxidation, microbial activities, mineralisation rates, and nutrient availability (Bazzaz, 1996). Regardless of precisely how in the study area an increase of finer soil particles negatively affects tree cover, our results suggest that changes in tree cover influenced antlion larvae in several ways. On one hand, an increase in tree cover may directly benefit antlion larvae because it enhances the capacity of trees to intercept sun and rain. As previously discussed, larvae often prefer shaded areas to avoid lethal temperatures (Marsh, 1987; Gotelli, 1993; Arnett & Gotelli, 2001; Gatti & Farji-Brener, 2002), and select sheltered areas to minimize the chance of pit destruction by rain (Cain, 1987; Gotelli, 1993; Morrison, 2004). Nonetheless, as tree cover increases, the amount of leaf litter that potentially can drop on the forest floor also increases. As discussed, leaf litter negatively affects antlions by damaging and/or covers pit traps. Therefore, tree cover has a positive direct effect on *M. crudelis* density by its capacity to intercept sun and rain, but a negative indirect effect through its capacity in generating leaf litter. Because finer soils affected tree cover negatively, the indirect effects of soil structure on antlion density can be negative or positive, depending whether the dominant effect of tree cover is to shelter larvae against sun and rain, or to damage their pits with leaf litter (Table 1).

The strength of indirect effects of soil structure on antlion abundance thus depends on the relative importance of soil temperature, rain interception, and the abundance of leaf litter. If the quantity of leaf litter on the forest floor represents a strong limitation for antlions, finer soils will offer the better scenario. In this substrate (i) pits are easy to built and have high capture success, and (ii) tree cover is diminished, thus the amount of leaf litter is reduced as well. However, if soil surface temperature and rainfall represent the strongest limitations rather than the amount of leaf litter, finer soils may have negative consequences on antlion abundance because they negatively affect tree cover, impoverishing the capacity of trees to intercept sun and rain. In this case, areas of finer soils may still be a better scenario for antlions depending on the relative importance of its direct benefits (i.e. a better pit construction and success) versus its indirect costs (i.e. a reduction in shaded areas). Furthermore, the relative importance between these direct and indirect interactions may vary throughout the year. For example, the availability of sheltered areas may be a strong selective pressure mainly in the rainy season. If trees are good shelters against rain, finer soils should be avoided during the rainy season because in this substrate tree cover is reduced. Conversely, in the dry season trees may have a greater effect as sources of leaf litter than as protection against sun (because the high abundance of deciduous plant species). In accord with this hypothesis, the direct effect of tree cover on antlion density as a source of shade was less than its indirect effect through leaf litter.

Experimental and correlative studies showed that antlions actively prefer building pits in finer soils. Consequently, the proportion of soil particle size has been proposed as the most important cue for habitat selection in this sit-and-wait predator (Lucas, 1982, 1985, 1989; Gatti & Farji-Brener, 2002; Botz *et al.*, 2003; Farji-Brener, 2003). However, habitat selection may also occur in response to certain characteristics that are associated with habitat quality indirectly. For example, if plant density varies with food availability or predation risk, variation in plant abundance may provide cues that facilitate habitat selection (Rolstad *et al.*, 2000). This work suggests that antlions may select patches of finer soils not only for its direct benefit, but also for its indirect benefit as sites with low litter fall. In other words, antlions may perceive the variation of soil structure as a signal of how much leaf litter this area will receive. This case illustrates how habitat selection can be modulated by indirect interactions.

Although our results suggest that soil structure is one of the major determinants of antlion density, it is important to discuss mechanisms that were not tested in this study. Competition and predation are two such mechanisms that often affect insect populations. Antlions could compete indirectly with plants for space, but our measurements revealed a high availability of bare ground outside from the measured plots. Similarly, competition for food is unlikely to affect density because ant abundance (the main source of food for antlions) is not at limiting factor in the study area (Lomascolo & Farji-Brener, 2001; Farji-Brener, 2003). In addition, there is little evidence of predation and parasitism on antlion larvae by other taxa (Lucas, 1985). Finally, the behaviour of adult antlions may affect larvae density if they often oviposit in fine-grained soils (Lucas, 1989). However, larvae are very mobile and often travel distances of several metres to relocate their pits (Heinrich & Heinrich, 1982; Crowley & Linton, 1999; Farji-Brener, 2003). Therefore, female oviposition behaviour may contribute to the origin of larvae density but not to its maintenance (Gotelli, 1993). In summary, as suggested by our results (70% of explained variance, Fig. 2), antlion density appears to be determined mainly by the direct and indirect effects of soil structure.

Trophic cascades – the effects of carnivores on plants mediated by herbivores – and apparent competition, or when an increase in the numbers of one prey decreases the numbers of another prey as a result change in the number of shared natural enemies, are among the most studied examples of indirect effects (Morris, 2002; Schmitz *et al.*, 2004). Our results demonstrated that changes in abiotic factors can also spread along other organisms and thus regulate indirectly the structure of populations. This emphasises the importance of distinguishing indirect from direct effects in order to fully understand the mechanisms behind patterns of animal abundance (Morris, 2002; Schmitz *et al.*, 2004). Understanding how these indirect interactions vary in large areas and over the long term is a major challenge for ecologists.

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