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Beetle succession and diversity between clothed sun-exposed and shaded pig carrion in a tropical dry forest landscape in Southern Mexico

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ABSTRACT

Over a 31-day period, the decomposition process, beetle diversity and succession on clothed pig (*Sus scrofa* L.) carcasses were studied in open (agricultural land) and shaded habitat (secondary forest) in Southern Mexico. The decomposition process was categorised into five stages: fresh, bloated, active decay, advanced decay and remains. Except for the bloated stage, the elapsed time for each decomposition stage was similar between open and shaded habitats, all carcasses reached an advanced decay stage in seven days, and the fifth stage (remains) was not recorded in any carcass during the time of this study. A total of 6344 beetles, belonging to 130 species and 21 families, were collected during the entire decomposition process, and abundances increased from fresh to advanced decay stages. Staphylinidae, Scarabaeidae and Histeridae were taxonomically and numerically dominant, accounting for 61% of the species richness and 87% of the total abundance. Similar numbers of species (87 and 88 species for open and shaded habitats, respectively), levels of diversity and proportions (open 49%; shaded 48%) of exclusive species were recorded at each habitat. There were significantly distinct beetle communities between habitats and for each stage of decomposition. An indicator species analysis ("IndVal") identified six species associated to open habitats, 10 species to shaded habitats and eight species to advanced decay stages. In addition, 23 beetle species are cited for the first time in the forensic literature. These results showed that open and shaded habitats both provide suitable habitat conditions for the carrion beetle diversity with significant differences in community structure and identity of the species associated to each habitat. This research provides the first empirical evidence of beetle ecological succession and diversity on carrion in Mexican agro-pastoral landscapes.

1. Introduction

Research on insect succession and community ecology may provide insight for carrion ecology, along with a source of evidence in medico-criminal investigations [1]. Studies of insect succession on carrion have been widely conducted in temperate zones, although in Neotropical ecosystems, where the vast majority of insects occur, only a small number of surveys have been reported, mostly from Argentina, Brazil, Chile and Colombia [2–10]. In general, the rate of decomposition, insect succession and composition of carrion communities are influenced by the geographical location, but also by environmental (biotic and abiotic) factors, namely micro-climate (local temperature and humidity conditions [11]), by the type and the physical state of the carcass remains [1], as well as by habitat loss and fragmentation [12]. An important implication of the spatial distribution of carrion relates to the tight dependency of their insect faunas, rendering them highly sensitive to habitat loss and change [12]. This is particularly true in tropical regions, where large areas of forest have been converted into complex landscape mosaics dominated by secondary forest fragments (relatively shaded-areas) and agro-pastoral systems (relatively open-areas [13]). What changes are taking place in the abundance, distribution, and diversity of specialised guilds as a result of habitat change and fragmentation in Neotropical systems?

In Mexico, a small number of descriptive reports on carrion insect succession have been published [14], but so far no survey has been attempted to determine faunal associations in relation to stages of decomposition, nor to assess the relative effects of changes in habitat suitability (e.g. differences between shaded and

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open habitats). The carrion insect fauna is represented predominately by two insect (taxonomic) orders, Diptera and Coleoptera [15]. Beetles occupy an ecologically diverse part of the carrion community, thus providing a wide spectrum of sources of potential evidence in medico-legal investigations [16,17]. In the last decade, the use of insects in forensic assessments has increased, although most research in forensic entomology has been focused on flies, and the use of beetle communities in forensic investigations remains very limited [17]. Beetle communities with forensic significance differ from region to region, but the most common carrion beetle families include Cleridae, Dermestidae, Histeridae, Scarabaeidae, Silphidae and Staphylinidae [15]. This is, to our knowledge, the first forensic entomological study in Mexico investigating patterns of ecological succession among carrion beetles.

Since several carrion beetle groups are known to be sensitive to micro-environmental changes (i.e., Carabidae, Scarabaeidae and Staphylinidae; [13,18–20]), this study aimed to describe, quantify and interpret beetle diversity and succession in pig carcasses exposed in contrasting habitats (open vs. shaded) from tropical Mexico. The work reported here specifically tests the following hypotheses (i) that different habitats (open and shaded) may have an effect on beetle diversity, community structure and succession patterns, and (ii) that each habitat and each decomposition stage will exhibit some level of taxonomic uniqueness and composition. In addition, the study discusses the usefulness of taxa associated to particular habitat and/or decomposition stages, and which of those can provide more accurate estimations of the minimum post mortem interval (PMImin). Ultimately, we provide detailed information on carrion beetle community and succession patterns that can be used as an entomological reference in other comparable Neotropical systems.

2. Materials and methods

2.1. Study site and experimental design

The study site was located on private ranch land (435 m.a.s.l., 16°32′55″ N, 92°59′04″ W, for convenience "Rancho Independencia"), 22 km SE of Tuxtla Gutierrez, Chiapas, Mexico. The average annual temperature and total rainfall of the study site were 21.9 °C and 992 mm, respectively. The climate corresponds to warm subhumid with rains in the summer (from May to October), April and September are the warmest and rainiest months, respectively [21]. The study landscape includes a range of natural and semi-natural habitats, including tropical dry forest, agro-pasture land, secondary forest and fallow land representing various stages of vegetative succession [13]. Two secondary forest sites were chosen (referred to as "shaded" habitat) and two agro-pasture land sites (the "open" habitat). The dominant vegetation in the area included *Acacia pennatula* Benth., *Bursera simaruba* (L.), *Cochlospermum vitifolium* (Willd.), *Cordia alliodora* (Ruiz and Pavón), *Guazuma ulmifolia* Lam. and *Gyrocarpus americanus* Jacq. [22].

Four domestic pig carcasses (*Sus scrofa* L.), weighing 9–12 kg were used as animal models to simulate human decomposition [23,24]. For each habitat, two recently deceased pigs were located 200 m from each other. Although the number and size of pigs allocated to each habitat were relatively small, this preliminary assessment was somewhat limited by two main reasons: (1) that medium-size pigs are commonly found across most pig farms in Mexico and therefore represented the most practical option as carcass samples (for comparable assessments see [2,5–8,25]), and (2) that, for ethical reasons, we could not deliberately increase the number of pigs (i.e., samples) in order to gain statistical power, as care was taken to follow the recommendations of our institutional ethical committee in handling animal samples.

Pigs were sacrificed by a sharp blow to the head and immediately dressed with two pieces of clothing (t-shirt and short pants) and placed in 100 cm × 70 cm × 40 cm grid-cages (2.8 m^3). Pigs were dressed because human victims are frequently found clothed [1]; additionally, previous surveys have suggested that clothing significantly influences decomposition rates and insect colonisation [11,26,27].

2.2. Beetle collection and identification

For each carcass, four pitfall traps (14 cm in diameter, one at each cardinal point) spaced 50 cm away from the carcass were buried at the soil level (for further details see Schoenly et al. [28]). Sampling was conducted from 9 August to 8 September 2008. On each sampling day, each trap was filled up with 10 cm^3 of 96% ethanol. Collections were made every day for the first seven days, every other day from days 9 to 17, and twice a week for the rest of the sampling period. Daily temperatures for each carcass were recorded using a probe thermometer (Ohaus ©, USA) for: (a) internal rectal carcass temperature, (b) ground-level temperature and (c) air temperature at 1.5 m above the ground. In addition, daily rainfall was measured using an exposed rain gauge (Taylor ©, USA). ANOVA tests were performed to identify differences among temperature conditions. Before performing statistical tests, data were tested for normality using Shapiro–Wilk tests [29].

The collected beetles were classified into family and morphospecies levels using specialised taxonomic keys [30–33], reference collections and expert advice (see Acknowledgments). Voucher specimens representing each species were deposited at the Entomological Collection of El Colegio de la Frontera Sur (ECOSC-E), San Cristóbal de las Casas, Mexico.

2.3. Decomposition stages

For this study, the five stages of carcass decomposition which had been previously defined were delimited: fresh, bloated, active decay, advanced decay and remains (for further details see Matuszewski et al. [34]).

2.4. Data analyses

Species richness estimates (ICE, Fisher's alpha values) and individually based rarefaction curves were performed for each habitat. In addition, the number of "rare" species was recorded (singletons and doubletons i.e., those for which only one or two individuals were recorded) (Novotny and Basset [35]). All calculations were performed using EstimateS 9.0.0 [36].

Beetle assemblage composition was compared between open and shaded habitats using non-metric multidimensional scaling ordination (NMDS [37]). Two-way PERMANOVA (permutational multivariate analysis of variance [38,39]) was used to test the independent and the interactive effect between habitat type and decomposition stages on community structure. The non-parametric PERMANOVA test calculates a pseudo-F (based on permutations) which is comparable to the F statistic from ANOVA and it is not affected by non-normal distributions of data [38]. The Bray–Curtis distance measure was used. Data $\log(x + 1)$ transformed were used for analyses, a procedure which is commonly applied to invertebrate assemblages to weight the importance of occasional large (and patchy) abundance values [37]. Multivariate analyses were performed in PAST v. 3.01 using 9999 permutations [40].

A measure of dominance was calculated using the proportion of individuals for the most common species in each habitat type (Berger–Parker index; [41]). The structure of species assemblages was examined using the comparison of the slope of the regression line of the relative abundance (log) and abundance-rank for the