*Journal of Tropical Ecology* (2006) **22**:359–370. Copyright © 2006 Cambridge University Press
doi:10.1017/S026646740600321X Printed in the United Kingdom

# Aggregation and coexistence of dung beetles in montane rain forest and deforested sites in central Peru

Finbarr G. Horgan[1]

Population Ecology Group, Department of Biology, University of New Brunswick, Fredericton, New Brunswick, E3B 6C2, Canada
(*Accepted 26 December 2005*)

**Abstract:** The 'aggregation model of coexistence' predicts that a strong and independent aggregation of species across ephemeral resource patches promotes species coexistence and maintains diversity. This study examines the role of aggregation in maintaining tropical dung beetle diversity and the effects of deforestation on aggregation patterns and diversity loss. Using clusters of pitfall traps, dung beetle aggregation was quantified in natural and disturbed habitat at nested temporal and spatial scales in central Peru. The results indicate that dung was colonized by a greater number of species, many of which were large, leading to a higher total beetle biomass in forest habitat than in deforested, farm habitat. Beetles were intraspecifically aggregated at each spatial scale examined. Habitat-type (forest/deforested) had no effect on the intensity of intra- or interspecific aggregation. Analyses of aggregation patterns revealed that dung beetle assemblages in forest habitat were generally saturated whereas in deforested habitat they were unsaturated. In general, interspecific aggregation was too weak relative to intraspecific aggregation to explain the high diversity of species in forest habitat. Other mechanisms, including resource partitioning are likely to play a greater role in maintaining the diversity of dung beetle assemblages in the region. These results also indicate that the loss of species from disturbed habitat has not been due to a breakdown in the aggregation mechanism.

**Key Words:** Aggregation model, biodiversity, biomass, coexistence, community structure, deforestation, habitat change, Peru, Scarabaeidae, species richness

## INTRODUCTION

Patchily distributed, ephemeral resources such as rotting fruit, carrion, fungi and dung are used for feeding and breeding by a diverse array of insects and other invertebrates (Hanski & Cambefort 1991a, Wertheim *et al.* 2000, Woodcock *et al.* 2002). The question of how so many species co-exist on such resources has been the focus of empirical and theoretical studies for decades (Atkinson & Shorrocks 1981, Hanski & Cambefort 1991b, c; Holter 1982, Remer & Heard 1998, Sevenster & van Alphen 1993, 1996; Shorrocks & Rosewell 1987).

One mechanism that has received considerable recent attention is the 'aggregation model of coexistence' (Hartley & Shorrocks 2002). This model suggests that the individuals of a single species, when clumped together, inhibit their own population growth to a greater extent than that of heterospecific populations. Therefore, even when species use the same type of resource, their coexistence is facilitated where the distribution of individuals differs across patches. The aggregation model has now gained considerable acceptance and has been applied to many patchy systems including carrion flies (Hanski 1987, Ives 1991), fruit flies (Sevenster & van Alphen 1993, 1996; Shorrocks & Rosewell 1987), mycophagous flies (Wertheim *et al.* 2000), dung beetles (Giller & Doube 1994, Hanski & Cambefort 1991c, Hutton & Giller 2004) and aquatic detritivores (Murphy *et al.* 1998). However, only recently has attention been drawn to the effects of human-induced habitat change on the functioning of the mechanism (Krijger & Sevenster 2001, Woodcock *et al.* 2002).

Dung beetles breed in dung pats where competition is frequently intense (Finn & Gittings 2003, Giller & Doube 1989, Horgan & Fuentes 2005). However, unlike flies and temperate dung beetles where competition mainly occurs in the larval stage (Finn & Gittings 2003, Ives 1991, Sevenster & van Alphen 1996), competition between tropical dung beetles is usually restricted to the adult stage (Giller & Doube 1989, Horgan & Fuentes 2005,

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[1] Current address: Teagasc, Oak Park Research Centre, Carlow, Co. Carlow, Ireland. Email: fhorgan@oakpark.teagasc.ie

**Table 1.** Details of forest and deforested, farm habitat at six sites near San Ramón where experiments were carried out during 2002.

| Sites | Altitude (m asl) | Slope (degrees) | Soil type[1] | Habitat description |
|---|---|---|---|---|
| San Ramón | | | | |
| El Tirol forest | 1000 | 40–80 | Red-clays, shale | Old second-growth forest reserve |
| CIP farm | 800 | 0–10 | Sandy-loam | Experimental farm with sweet potato (*Ipomoea batatas*) and pasture |
| Shimiyacu | | | | |
| Upper Shimiyacu forest | 1500 | 50–80 | Red and grey clays | Continuous intact forest, adjacent to Pui Pui Forest Reserve |
| Huaynarupay farm | 1300 | 30 | Clays | Recently cleared smallholding (*c.* 1–6 y) |
| La Mosela | | | | |
| La Mosela forest | 1200 | 30–60 | Sandy-loam | Catchment of Siete Casas Brook; old-growth forest patch (*c.* 10 ha) |
| La Mosela farm | 1300 | 30–80 | Clay-loam | Smallholding recently cleared of 6-y-old secondary forest (*c.* 2 y) |
| La Perla | | | | |
| Signori forest | 1300 | 50–80 | Deep-loam, some clay | Regenerated forest on abandoned coffee plantation (*c.* 5 ha) |
| Signori farm | 1300 | 0–40 | Deep-loam | Farm dedicated to banana cultivation (> 40 y) |
| Alta Cajacuri I | | | | |
| Roman forest | 1300 | 60–80 | Sandy-loam-rocky | Edge of continuous, largely-intact forest |
| Roman farm | 1200 | 50 | Sandy-loam | Recently cleared smallholding (*c.* 1–4 y) |
| Alta Cajacuri II | | | | |
| Gallegos forest | 1200 | 60 | Sandy-loam-rocky | Forest patch (*c.* 1 ha), some selective logging. Connected to continuous forest at higher altitudes by a narrow belt of native vegetation. |
| Gallegos farm | 1300 | 80 | Sandy-loam-rocky | Recently cleared smallholding (*c.* 1–4 y) |

[1] Determined visually from soil pits.

Peck & Forsyth 1982). By burying or hiding dung, and through highly developed parental care, most tropical dung beetles ensure that their larvae do not compete with each other or with the larvae of other dung beetle species (Doube 1990, Halffter & Edmonds 1982). The long-term coexistence of tropical dung beetles is therefore dependent on females encountering dung pats or other substrates (henceforth referred to as resource patches) with low densities of superior competitors, such that a significant amount of resource can be procured for egg laying. For some species, the patch should also include a conspecific male, since male–female cooperation in nest building occurs in many tropical dung beetles (Doube 1990, Halffter & Edmonds 1982). The success of beetles in locating such patches depends on the total number of beetles in the assemblage and their combined biomass relative to resource availability, which vary spatially and temporally.

The present study assesses whether the aggregation model of coexistence operates to promote the coexistence of dung beetles by quantifying intra- and interspecific aggregation of beetles in tropical montane habitat of the Peruvian Andes. The aggregation model proposes that competitively inferior species are maintained in assemblages because they normally encounter uninhabited or low-density patches. Where the number of beetles and their combined biomass are low relative to resource availability, resource patches are likely to be unsaturated and the probability of an inferior competitor finding a low-density patch increases. Such conditions may arise more frequently in disturbed than in natural habitat because disturbed habitat generally has fewer species and a lower total biomass of beetles per patch (Andresen 2002a, Horgan 2005a, Howden & Nealis 1975, Janzen 1983, Klein 1989). However, spatial variation in the colonization of resource patches brought about by variable microclimatic conditions may be lower in disturbed habitat, which is often topographically and structurally more homogeneous than forest habitat (see Vandermeer *et al.* 1998). Depending on the relative extent of habitat homogeneity, this may counteract the effects of a lower abundance and biomass of beetles and could lead to a lower prevalence of negative interspecific aggregations in disturbed habitat. If aggregation maintains dung beetle species richness then the overall magnitude of negative intraspecific aggregations should be notably higher in the more species-rich forested areas. This study examines these predictions by comparing aggregation patterns at nested temporal and spatial scales in native forests and derived farms. As such, this study also assesses whether changes in aggregation patterns could play a role in the loss of species associated with habitat destruction.

## STUDY SITES

Experiments were carried out near San Ramón in the Department of Junín, Central Peru (11°03′–11°10′S, 75°18′–75°24′W). Sampling was carried out at six sites that each included forest fragments or continuous forest with adjacent farms and smallholdings (properties at a distance from the owner's residence). Details of the sites are presented in Table 1 (for further information see Horgan 2005a). Distances between 1 and 15 km separated each site. The mean annual temperature during the year of study (2002) was 25.4 °C and total annual precipitation was 2091 mm with a dry period between May and September (data from the International Potato Centre (CIP) weather station, San Ramón at 820 m asl). The Andean slopes are noted for their diversity of mammalian fauna (Emmons 1997) and many forest species make night-time incursions into open farms (personal communication with local farmers and hunters); dung of these species is deposited in both forest and deforested habitat.

## STUDY SPECIES

Many neotropical beetles utilize dung for feeding and reproduction. This study focuses only on true dung beetles of the family Scarabaeinae. These are separated into four main groups based on their reproductive and nest-building behaviours (Doube 1990, Halffter & Edmonds 1982): Ball rollers (telocoprids) form balls of dung, which they roll some distance from the source pat. The dung is then buried in a superficial tunnel or under leaf litter and a nest is constructed. Tunnellers (paracoprids) form tunnels directly beneath the source dung pat. The tunnels are then provisioned with dung and eggs are laid. Dwellers (endocoprids) do not relocate the dung but instead construct simple nests within or beneath the dung pat. Some species oviposit directly on the dung pat. A number of species use dung that has been buried by others. These have been termed 'kleptocoprids' (Doube 1990). In the Neotropics the vast majority of dung beetles are rollers or tunnellers (Gill 1991).

## METHODS

### Spatial patterns

Pitfall trapping was used to examine aggregation at three spatial scales including between traps (metres), between clusters of traps (tens of metres) and between sites (kilometres) in forest and deforested habitat. Thirty traps were set out in each habitat at each site (60 per site). Traps in each type of habitat were set out in five clusters of six traps. The location of clusters was decided arbitrarily. Clusters were separated by 50–100 m whereas the individual traps within each cluster were each separated by approximately 7 m in two rows of three traps. This spatial arrangement was designed to simulate mammalian defecation patterns and assumes that mammalian dung is normally spatially clumped (Andresen 2002b, Horgan 2005b). In April 2002, the Roman forest site was partially cleared so that only two clusters remained under forest at the site for October–December sampling.

Aggregation patterns were also examined at two temporal scales including days and months. Trapping was conducted on six consecutive days at two of the sites (San Ramón and La Mosela) in both forest and deforested habitat. Furthermore, trapping was carried out in both habitat types at all six sites on at least two occasions: once in April or May of 2002 and once between October and December of the same year.

Pitfall traps were used because they capture beetles from all functional groups; however, pitfalls do not allow for interactions between beetles, or between the beetles and the dung pat and, therefore, exclude the possibility of beetles rejecting the resource (Giller & Doube 1994, Horgan 2005b). Therefore, this study assumes that once a beetle arrives at a dung pat, it will rarely leave without utilizing a portion of it, even in the presence of large numbers of competitors. This has been borne out by experimental evidence at least for tunnellers, which are the dominant functional group in the region (Horgan 2005b).

Traps consisted of plastic cups 10 cm deep and 10 cm in diameter. Small holes were made at the base of each cup for drainage and cups were dug into the ground so that the mouth was flush with the ground surface. A tightly fitting plastic funnel, with a 3–4-cm-diameter aperture that permitted the capture of large dung beetles, was placed over the mouth of each cup. Human dung was used as bait. The fresh dung was homogenized, measured out in 25-ml quantities, wrapped in muslin and frozen before each experiment. Old baits were replaced with fresh baits after each 24-h period. Different batches of dung were used on different days; however, the baits used on each day and at each site (including forest and adjacent deforested habitat) were always from the same batch. Dung baits were placed directly in the cups to reduce interference from scavenging mammals. Traps were set in the evening between 16h00 and 18h00 and collected 24 h later. All beetles in the traps were identified and counted. All living beetles were released to the same sites except for voucher specimens, and on days of continuous trapping when they were released at a distance of *c*. 2 km from the respective sites. To estimate dry weights, the first 20 specimens of each morphospecies captured in the traps were dried in a forced-draught oven at 60 °C until a constant weight was attained.

### Data analysis

The effects of habitat and trapping period on total assemblage biomass, and species richness were analysed using two-way split-block ANOVAs with trap-clusters as the sampling unit. Community-level indices (see below) were analysed using three-way ANOVAs removing the effect of blocks. Biomass data were log-transformed and species richness was square-root-transformed based on distributions of the data. Residuals were plotted following analyses to ensure normality and homogeneity. Species richness at each site was adjusted using rarefaction (Ecosim 7.0, http://homepage.together.net/ ∼gentsmin/ecosim.htm) to standardize for differences in sample sizes (26 to 390 beetles habitat per site $d^{-1}$).

Spearman correlations were used to examine the conspicuousness of baits at each microsite (i.e. trap position) and cluster position over successive days and between seasons. Conspicuousness is a measure of whether traps or clusters at a specific location in a given habitat within each site were more likely to capture beetles than traps at other locations in the same habitat and site. Because baits were homogenized, significant positive correlations between traps catches on successive days would indicate a consistent gradient of trap effectiveness that depicts underlying differences in trap conspicuousness due to different microhabitat conditions at specific trap locations.

A number of indices have been developed to examine aggregation patterns and persistence criteria for species utilizing discrete resource patches (Ives 1991, Krijger & Sevenster 2001, Sevenster 1996). Slight adaptations of these indices were used here for the special case of dung beetles that either feed or breed at resource patches, which differs from fly communities (for which the indices were largely devised) that undergo a complete generation wholly within the resource patch. Because the amount of dung used by neotropical dung beetles at each successful colonization event is largely proportional to the beetle's body size (Doube 1990, Horgan 2001), complications of the model due to a poor understanding of the effects of clutch size (see Remer & Heard 1998) do not arise. This study is concerned with the effects of resource pre-emption during scramble competition on the coexistence of adult beetles.

The strength of conspecific aggregation was determined using the aggregation index J (Ives 1991) (Appendix 1). The value of J indicates the proportional increase in the level of crowding by conspecifics, attracted to the same trap, cluster of traps, or site, above that expected if beetles were randomly distributed (Ives 1991). The significance of departure of J from zero within sites was examined using the chi-square test. However, the significance of deviations was not tested at smaller scales as this would result in a biased chi-square calculation because sample sizes were small (six traps per cluster, five clusters per site) and many species were rare (Zar 1984).

Ives' measure of interspecific aggregation, C, was used to measure interspecific associations of beetles among traps, clusters of traps and sites (Ives 1991) (Appendix 1). The value of C indicates the proportional increase in the levels of crowding due to heterospecific competitors in the same trap, cluster or site relative to that expected if species were randomly distributed (Ives 1991). Because species vary considerably in size, the relative contributions made by different species to competition and resource depletion were incorporated into the analyses by using beetle biomass when calculating C. Interspecific associations between each of the most abundant species and a 'super-species' complex, comprising all the remaining species in the data set, were determined, i.e. $C_{xy}$ (Sevenster 1996, Sevenster & van Alphen 1996, Shorrocks & Rosewell 1986, 1987). Spearman rank correlations were used to test the significance of departure of $C_{xy}$ from zero. Multidimensional scaling (MDS), an ordination technique for examining structure in proximity matrices, was used to examine patterns in J and $C_{xy}$. Euclidian distances between species-habitat combinations (columns) and aggregation indices at nested scales (rows) were used as proximity measures, and stress values were examined to assess the model goodness-of-fit.

The relative effect of competitor aggregation on species coexistence was measured using $T_{xy}$ (Sevenster 1996) (Appendix 1). $T_{xy}$ has been called 'the necessary and sufficient condition for coexistence of species x and the super-species y'. For coexistence to occur, the average competitive inhibition of y on x must be less than the inhibition caused by y on itself; in this way species x is inhibited less by species y than y is by itself, allowing species x to increase when rare (Sevenster 1996). T has values from zero to infinity. Theoretically, values below unity (i.e. below a value of 1) predict long-term persistence of a given species x, while values greater than unity predict its demise (Sevenster 1996). However, even if the condition for coexistence is violated in the short-term it may on average be below unity in the long-term (Woodcock *et al.* 2002). Therefore, the utility of this index in explaining species presence/absence in communities is severely restricted due to the impracticality of attaining sufficient good-quality data to make accurate predictions. For this reason $T_{xy}$ is regarded here as an index of competition pressure that is specific in time and space. Beetle biomass was used in calculating $T_{xy}$ for the same reasons as outlined above.

J, $C_{xy}$ and $T_{xy}$ were determined for each of the common species in each habitat at each site. However, since this study compares habitat-related, community-level patterns, the averages of the species-specific J, $C_{xy}$ and $T_{xy}$ for each habitat at each site were required. Therefore, $J_{x,-x}$, $C_{x,-x}$ and $T_{x,-x}$ were determined for both habitat types at each site as the geometric means of species-specific J, $C_{xy}$ and $T_{xy}$ respectively (Krijger & Sevenster 2001) (Appendix 1). Linear regression was used to examine the relationship between $T_{x,-x}$ and both species richness and biomass across sites.

## RESULTS

### Colonization patterns

A total of 5006 beetles from 45 species (excluding Hybosoridae and Aphodiinae) were captured during this study. Further details on assemblage composition at the sites can be found in a related article (Horgan 2005a). Many of the species were rare (fewer than 10 individuals) (Table 2). Only 21 species were sufficiently common for analyses of aggregation patterns (i.e. number of beetles > number of traps, clusters or sites), but total biomass of all 45 species was used in estimating community-level parameters.

Habitat significantly affected the number of species and total beetle biomass in trap clusters, but trapping period and interactions had no statistically significant effect (Species richness, site: $F_{5,5} = 0.94$, $P = 0.526$, habitat: $F_{1,5} = 12.9$, $P = 0.016$, season: $F_{1,5} = 1.80$, $P = 0.237$, habitat × season $F_{1,5} = 0.43$, $P = 0.540$; Total beetle biomass, site: $F_{5,5} = 1.24$, $P = 0.410$, habitat: $F_{1,5} = 6.73$, $P = 0.049$, season: $F_{1,5} = 2.31$, $P = 0.189$, habitat × season $F_{1,5} = 1.21$, $P = 0.321$) (Figure 1a, b). Biomass and species richness were highly correlated at the sites during each trapping period (Pearson correlation: April–May, $r = 0.75$, $df = 12$, $P < 0.005$; October–December, $r = 0.82$, $df = 12$, $P < 0.001$).

### Microsite conspicuousness

There was no evidence of any particular traps or clusters of traps having predictably higher or lower beetle captures for any given habitat within each site (i.e. conspicuousness). The number of beetles captured fluctuated at San Ramón and La Mosela over the 6-d periods. The number of significantly positive correlations between successive trap catches within each cluster and between clusters at each site were generally low for each of the common beetle species (i.e. within clusters: 31 positive ($\alpha = 0.1$) from a total of 485 correlations, 8 of 103 on day 1, and within sites: 14 positive ($\alpha = 0.1$) from a total of 286 correlations, 6 of 56 on day 1). The proportion of positive correlations was uniform across nested time periods (Komolgorov-Smirnov tests: $0.734 \geq P \leq 0.997$).

### Species-level aggregation patterns

All species were intraspecifically aggregated between traps, clusters and sites for both habitat-types and during both sampling periods ($J_{trap} = 0.15$ to 5.89, $J_{cluster} = 0.04$ to 3.63, and $J_{site} = 0.17$ to 6.86). In all but four of the cases where the minimum condition for analyses occurred, aggregation between traps within sites was significantly different from zero (Table 2).

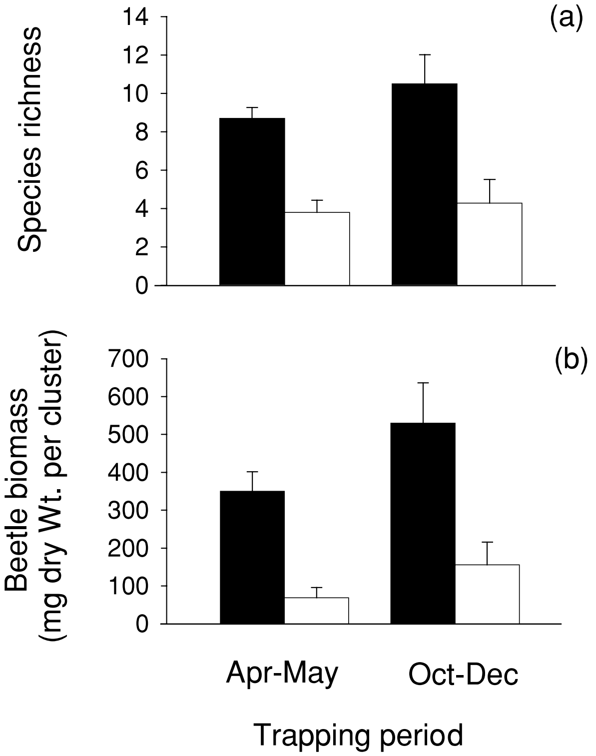

**Figure 1.** Mean species richness per trap cluster (a) at forested (solid bars) and deforested habitat (open bars) near San Ramón, Peru, during the late rainy season in April–May and the early rainy season in October–December 2002 with the mean total beetle biomass at the sites (b). Data are from six forests each with an adjacent deforested area. Bars represent 1 SE.

Figures 2a and 2b are MDS plots based on aggregation at three spatial scales for 14 species at forested sites and 9 species at the deforested sites (not all species are included in each section of Figure 2). Open-field and forest species separated along dimension 2 in the April–May samples (stress values < 0.001) (Figure 2a) but not in the October–December samples (Figure 2b). Dimension 2 is directly related to the strength of aggregation between clusters and sites relative to that between traps within clusters. Species with values below zero on this scale were highly aggregated between traps, while those above zero had low levels of aggregation between traps relative to aggregation at the other spatial scales.

Associations between each species and the heterospecific species complex varied between scales ($C_{xy\text{-}trap} = -0.38$ to 1.92, $C_{xy\text{-}cluster} = -0.37$ to 0.43, and $C_{xy\text{-}site} = -0.88$ to 1.24). Significant negative interspecific associations between each of the most common species and the super-species complex were apparent at every scale in both forest and deforested habitat (Table 3). However, positive associations were more common. Figures 2c and 2d are MSD plots based on interspecific associations between species. Dimension 1 indicates the relative strengths of $C_{xy}$ at the trap and cluster levels relative

**Table 2.** Total number of dung beetles captured in pitfall traps baited with human dung in forest and deforested, farm habitat at six sites near San Ramón, indicating the occurrence of species at the sites and the prevalence of significant departure of J from zero for 16 abundant species at forested sites and nine abundant species at farm sites (numbers in parentheses).

| Species | No.[1] | Dry wt (mg)[2] | No. from forest | No. forest sites (sig.J/tests)[3] | No. from farms | No. farm sites (sig.J/tests)[3] |
|---|---|---|---|---|---|---|
| Large tunnellers | | | | | | |
| *Coprophanaeus t. telamon* Erichson | 3 | 331 ± 9 | 4 | 3 | 13 | 1 |
| *Diabroctis mimas mimas* (L.) | 4 | 555 | 0 | 0 | 1 | 1 |
| *Dichotomius adrastus* (Harold) | 13 | 350 ± 18 | 66 | 1(1/1) | 9 | 1 |
| *Dichotomius fissus* (Harold) | 14 | 188 ± 9 | 2 | 1 | 0 | 0 |
| *Dichotomius* sp. 1 | 15 | 242 ± 14 | 649 | 5(4/4) | 135 | 4(1/1) |
| *Dichotomius* sp. 2 | 16 | 87 ± 4 | 496 | 5(5/5) | 87 | 4(1/2) |
| *Dichotomius* sp. 3 | 54 | 255 | 2 | 1 | 0 | 0 |
| *Ontherus alexis* (Blanchard) | 18 | 64 ± 5 | 168 | 6(1/2) | 64 | 3(1/1) |
| *Ontherus pubens* Génier | 20 | 62 ± 5 | 0 | 0 | 24 | 2 |
| *Oxysternon conspicullatum* Weber | 5 | 356 ± 20 | 5 | 3 | 34 | 1(1/1) |
| *Oxysternon smaragdinum* Olsoufieff | 6 | 177 ± 48 | 22 | 5 | 7 | 4 |
| *Phanaeus chalcomelas* (Perty) | 1 | 225 ± 18 | 307 | 5(3/3) | 0 | 0 |
| *Phanaeus meleagris* Blanchard | 2 | 250 ± 16 | 2 | 1 | 0 | 0 |
| Small tunnellers | | | | | | |
| *Ateuchus* cf. *laevicollis* Harold | 17 | 30 ± 15 | 129 | 5(1/1) | 0 | 0 |
| *Ateuchus* sp. 2 | 53 | 3 ± 1 | 17 | 1 | 0 | 0 |
| *Onthophagus* gr. *clypeatus* Blanchard | 22 | 10 ± 2 | 93 | 6(1/2) | 46 | 6(1/1) |
| *Onthophagus haematopus* Harold | 23 | 8 ± 2 | 17 | 5 | 4 | 3 |
| *Onthophagus* sp. 1 | 24 | 10 ± 1 | 0 | 0 | 10 | 1 |
| *Canthidium* sp. 1 | 38 | 5 ± 4 | 382 | 6(5/5) | 18 | 4 |
| *Canthidium* sp. 2 | 39 | 3 ± 1 | 0 | 0 | 68 | 4(0/1) |
| *Canthidium* sp. 3 | 40 | 10 ± 2 | 3 | 1 | 0 | 0 |
| *Canthidium* sp. 4 | 41 | 3 ± 1 | 25 | 1(1/1) | 0 | 0 |
| *Canthidium* sp. 5 | 42 | 5 ± 1 | 3 | 4 | 0 | 0 |
| *Canthidium* sp. 6 | 43 | 32 ± 16 | 4 | 1 | 0 | 0 |
| *Uroxys* sp. 1 | 52 | 10 ± 1 | 86 | 5(2/2) | 8 | 1 |
| Large ball rollers | | | | | | |
| *Deltochilum burmeisteri* Harold | 10 | 298 ± 11 | 8 | 1 | 0 | 0 |
| *Deltochilum laevigatum* Balthasar | 11 | 66 ± 12 | 31 | 1 | 8 | 1 |
| *Deltochilum orbiculare* Lansberge | 9 | 320 | 3 | 1 | 0 | 0 |
| *Deltochilum* sp. 1 | 51 | 61 ± 4 | 6 | 1 | 0 | 0 |
| *Streblopus punctatus* (Balthasar) | 21 | 65 ± 3 | 1 | 1 | 0 | 0 |
| Small ball rollers | | | | | | |
| *Canthon laesus* Erichson | 28 | 27 ± 2 | 303 | 2(3/3) | 3 | 1 |
| *Canthon lituratus* Germar | 35 | 9 ± 1 | 0 | 0 | 439 | 5(2/3) |
| *Canthon luteicollis* Erichson | 29 | 25 ± 3 | 0 | 0 | 224 | 3(2/2) |
| *Canthon subhyalinus* Harold | 32 | 8 ± 2 | 28 | 3(1/1) | 9 | 2 |
| *Canthon virens chalybaeus* Blanchard | 33 | 19 ± 1 | 0 | 0 | 305 | 6(3/3) |
| *Canthon* sp. 1 | 30 | 15 ± 1 | 6 | 2 | 32 | 2 |
| *Canthon* sp. 2 | 34 | 6 ± 2 | 13 | 2 | 0 | 0 |
| *Canthon* sp. 3 | 55 | 6 ± 2 | 8 | 2 | 0 | 0 |
| *Pseudocanthon xanthurum* (Blanchard) | 50 | 3 ± 1 | 0 | 0 | 10 | 1 |
| *Scybalocanthon trimaculatus* (Schmidt) | 36 | 11 ± 7 | 27 | 3(1/1) | 0 | 0 |
| *Sylvicanthon bridarollii* Martínez | 37 | 39 ± 21 | 138 | 6(1/1) | 0 | 0 |
| Eurysternini dwellers | | | | | | |
| *Eurysternus caribaeus* (Herbst) | 47 | 79 ± 9 | 109 | 6(1/2) | 16 | 4 |
| *Eurysternus velutinus* Bates | 46 | 103 ± 18 | 2 | 2 | 8 | 1 |
| *Eurysternus* sp. 1 | 48 | 10 ± 4 | 252 | 6(2/2) | 1 | 1 |
| *Eurysternus* sp. 2 | 49 | 11 ± 1 | 6 | 2 | 0 | 0 |
| Total individuals | | | 3423 | | 1583 | |
| Total species | | | 37 | | 26 | |

[1] Numbers refer to numbered voucher specimens held at the Museo de Historia Natural and at the Department of Entomology, Universidad Agraria La Molina, Lima, Peru.

[2] Mean dry weight ± SE: specimens of undetermined sex ($5 \geq n \leq 20$).

[3] Only sites where number of beetles ≥ number of traps are included (i.e. minimal condition for analysis). Numbers in parentheses = number of times J values for species within sites were significantly different from zero (chi-squared test: $P \leq 0.05$)/number of times minimal condition for analyses occurred.

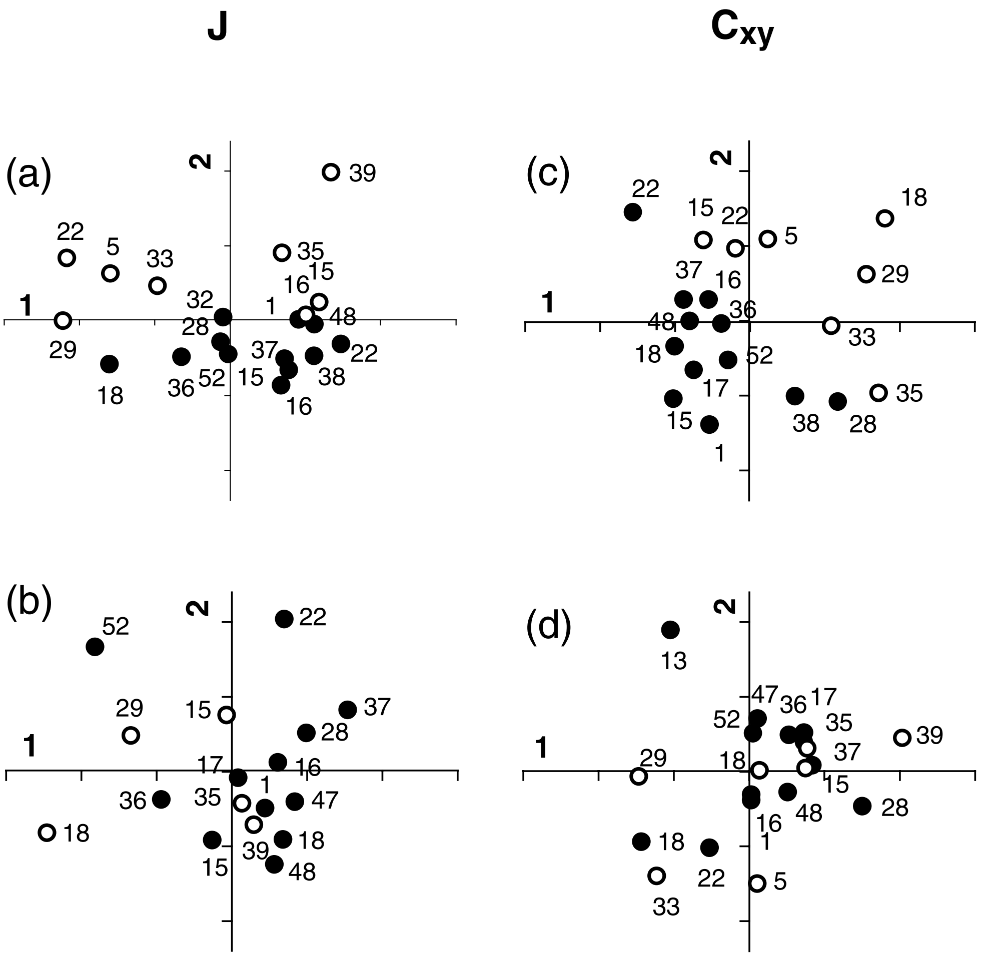

**Figure 2.** MDS plots of intraspecific aggregation, J, for 23 species-habitat combinations at three spatial scales in (a) April–May and (b) October–December, with interspecific aggregation, $C_{xy}$, for 22 species-habitat combinations at three spatial scales in (c) April–May and (d) October–December. Solid circles = forest habitat, open circles = deforested habitat. Numbers correspond with species' voucher numbers in Table 2.

**Table 3.** Number of significant positive and negative associations between each of the most abundant species and the super-species complex at three spatial scales. At deforested sites there were nine common species, and at forest sites there were 12 (April–May) to 14 common species (October–December).

| | Trap | | Cluster | | Site | |
|---|---|---|---|---|---|---|
| | Forest | Farm | Forest | Farm | Forest | Farm |
| Number of significantly positive $C_{xy}$ values | 46 | 28 | 33 | 23 | 17 | 10 |
| Number of significantly negative $C_{xy}$ values | 6 | 2 | 6 | 8 | 12 | 4 |
| Number of associations tested | 166 | 56 | 141 | 46 | 29 | 14 |

to that at the site level, whereas dimension 2 largely represents the relative strength of $C_{xy}$ at the site level. In Figure 2c, based on April–May data, open-field species occur at the top right-hand corner of the graph indicating high overall $C_{xy\text{-site}}$, and relatively higher $C_{xy\text{-trap}}$ and $C_{xy\text{-cluster}}$ than forest species (stress values $< 0.001$). Patterns generated from the October–December data were irregular and could not be interpreted (Figure 2d).

Values of $T_{xy}$ were generally high at all spatial scales and particularly at the site scale in October–December. Fourteen of the 25 species-habitat combinations had values of $T_{xy}$ greater than 1 at some scale, but no species had values greater than 1 at all three scales ($T_{xy\text{-trap}} = 0.46$–$1.10$, $T_{xy\text{-cluster}} = 0.70$–$1.03$, and $T_{xy\text{-site}} = 0.46$–$1.83$).

## Community-level aggregation patterns

At the community level, intraspecific aggregation was greater between traps within clusters than between clusters (Figure 3a, Table 4). No season or habitat

**Table 4.** F-values from three-way ANOVAs for community-level indices, see also Figure 3.

| Community-level Index | F-value[1] | | | | | | |
|---|---|---|---|---|---|---|---|
| | Scale | Season | Habitat | Scale × Season | Scale × Habitat | Season × Habitat | Scale × Season × Habitat |
| $J_{x,-x}$ | $43.1^{***}$ | $0.365^{ns}$ | $2.30^{ns}$ | $0.205^{ns}$ | $1.05^{ns}$ | $0.606^{ns}$ | $0.449^{ns}$ |
| $C_{x,-x}$ | $1.76^{ns}$ | $0.001^{ns}$ | $0.323^{ns}$ | $0.228^{ns}$ | $1.23^{ns}$ | $3.71^{ns}$ | $0.776^{ns}$ |
| $T_{x,-x}$ | $22.9^{***}$ | $4.53^{*}$ | $0.001^{ns}$ | $1.99^{ns}$ | $6.22^{*}$ | $0.252^{ns}$ | $0.291^{ns}$ |

[1] df = 1,32; $P \leq 0.001$, ***; $P \leq 0.05$, *; $P > 0.05$, ns.

effect, two-way or three-way interaction was significant. There was no significant effect of scale, habitat, season, two-way or three-way interactions on the magnitude of community-level interspecific aggregation (Figure 3b, Table 4). $T_{x,-x}$ was greater between clusters than between traps within clusters and was significantly higher in October–December. There was a significant interaction between habitat and scale in determining $T_{x,-x} \cdot T_{x,-x}$ was higher in forested habitats than in the deforested habitats at the cluster scale, but lower in forested habitats at the trap scale. However, $T_{x,-x}$ was not significantly different across scales in deforested, farm habitat (Figure 3c, Table 4).

$T_{x,-x}$ for traps within sites (i.e. including together both the scales of traps within clusters and clusters within sites) for the April–May data was directly related to species richness ($y = 0.27 + 0.05x$, $R^2 = 0.37$, $P = 0.037$) and log-transformed community biomass ($y = 0.07 + 0.33x$, $R^2 = 0.51$, $P = 0.009$). However, there was no apparent relationship between $T_{x,-x}$ and either species richness or biomass for the October–December data.

## DISCUSSION

All of the beetles studied here were intraspecifically aggregated at some spatial scale. Intraspecific aggregation was often greater than interspecific aggregation ($C_{xy} < 0$), such that spatial patterns are expected to contribute to dung beetle coexistence. Similar results have been shown for other tropical and subtropical dung beetle communities (Cambefort 1991, Giller & Doube 1994, Lobo & Montes de Oca 1997) but not for adult temperate dung beetles (Holter 1982, Hutton & Giller 2004). Aggregation may be more important for the adults of tropical dung beetles than for temperate species. This is because competition in tropical dung beetles occurs mainly in the adult stage; the adults of tropical species actively pre-empt resources for their larvae thus avoiding larval competition, whereas in temperate dung beetles, competition between larvae may be intense (Finn & Gittings 2003). In spite of significant aggregation of beetles in this study, community-level T was generally higher in species-rich, forested sites indicating a greater

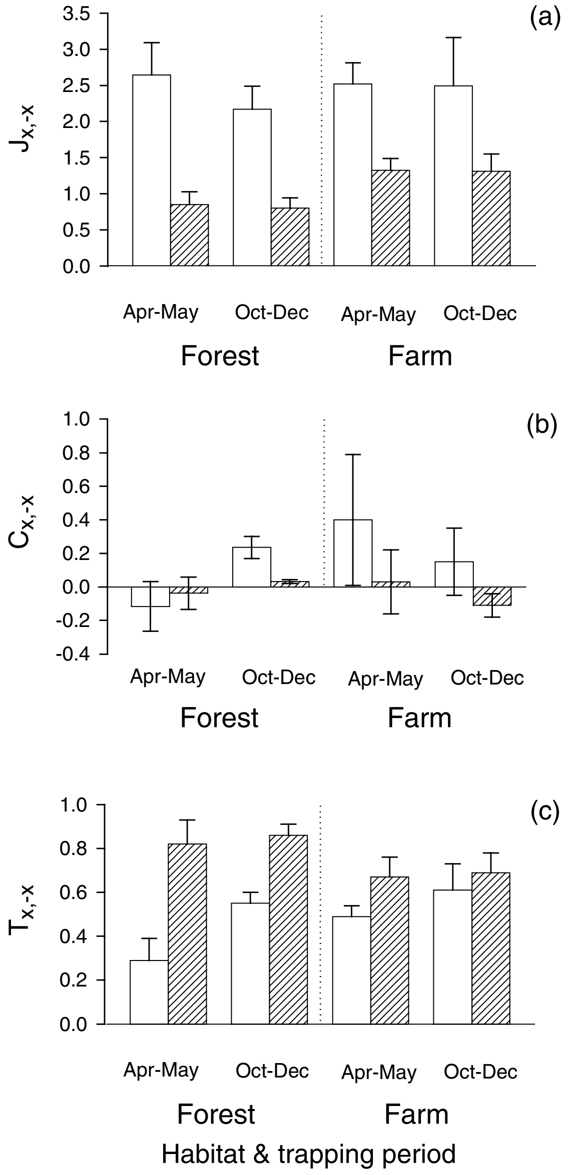

**Figure 3.** Community-level intraspecific aggregation (a), community-level interspecific aggregation (b) and the 'necessary condition for coexistence' (c) for dung beetle communities at two spatial scales including patches within clusters (shaded), and between clusters (open) at different sites. Data are from six forest and six deforested, farm sites where trapping was carried out during the late (April–May) and early (October–December) rainy season. Bars indicate 1 SE.

turnover of species at those sites and a failure of the aggregation mechanism to explain the greater diversity of species in the forests compared to the deforested, farmed sites. These results also suggest that the loss of dung beetle species from disturbed habitat is unlikely to result from a breakdown in the aggregation mechanism.

## Causes of aggregation

To date, a number of mechanisms have been proposed to explain the aggregated distributions of insects using patchy, ephemeral resources, but there is a general lack of evidence for any mechanism (Giller & Doube 1994, Gittings & Giller 1998, Hanski & Cambefort 1991c, Holter 1982, Remer & Heard 1998). Aggregation may be caused by intrinsic characteristics of the species in question, including searching behaviours, flight patterns, size and metabolic rates (Sevenster & van Alphen 1993). Tropical dung beetles may generally respond to pheromones, or a mix of pheromones and dung odours that cause aggregation since they often demonstrate high levels of parental care (Halffter & Edmonds 1982). Aggregation might also be due to beetle responses to resource patch quality, habitat quality, or interactions between the two, i.e. ‘conspicuousness’ (Sevenster & van Alphen 1993) or ‘findability’ (Gittings & Giller 1998). In some cases, patch quality can vary even where attempts have been made to ensure homogeneity (Ives 1991).

In this study, the results from consecutive days of pitfall trapping suggest that microtopographical differences in trap locations either had no effect on beetle colonization, or the effects were not consistent over consecutive days. This differs from the results of Giller & Doube (1994) where certain traps consistently captured more beetles during consecutive days of sampling in South African pastures. Pastures are structurally more homogeneous than forests, and Giller & Doube (1994) suggested that previous patterns of cattle grazing, and thus defecation could have influenced trap catches. In a similar manner, naturally occurring droppings at the sites studied here could have influenced trap catches but with effects that were sustained over a relatively short period because decomposition was generally fast, i.e. 100 ml of dung disappears in less than 1 wk at all sites studied here and throughout the year (Horgan 2005a). Furthermore, the relative distribution of naturally occurring patches and microtopography are likely to interact with each other and with ambient climatic conditions such that the relative conspicuousness of traps changes with changing wind-force, wind direction or rainfall. The distance between adjacent dung pats also affects beetle colonization and the strength of dung beetle aggregation in tropical forests, presumably because interference between odour plumes affects beetle foraging behaviours (Horgan 2005b). These complications in standardizing habitat and resource patches, even in experimental systems, are indicative of the difficulties in successfully separating the aggregation model from classical resource partitioning mechanisms.

## Aggregation in forest and deforested habitat

The relative strengths of aggregation at different spatial scales differed according to habitat type and trapping period. An apparent trend in the results of this study is a shift from aggregation-related dynamics in April–May to dynamics without a strong influence of aggregation in October–December, in spite of only a slight increase in biomass and species richness at the sites in the October–December trapping period. It is difficult to suggest why this occurs since the mechanisms leading to aggregation are still unknown. Possible causes may be related to changes in the physiological condition (including reproductive condition) of the beetles between the sampling periods, fluctuating natural patch densities at the sites, or changes in habitat structure between trapping periods. Also, the numbers of empty or low-density patches (traps with zero, one or two beetles) are highly correlated with J. Even though biomass increased only slightly during the early rainy season, low-density patches were rare so that the magnitude and differences between the levels of aggregation at different spatial scales were reduced. This implies that competition refuges were less common for inferior competitors at each of the three spatial scales at the beginning of the rainy season and particularly at the forest sites.

During the April–May period, beetles in deforested habitat aggregated to a greater extent at the cluster and site scales than among traps within clusters when compared to forest species. Species in deforested areas were generally more positively, interspecifically aggregated at the cluster scale while forest species showed more positive interspecific aggregation at the site scale. Site-specific differences in the grain of habitat heterogeneity at larger scales may have led to these differences in aggregation patterns. During the drier months, species at the deforested sites were aggregated between traps and clusters. Most of the sites were fairly small, usually of 1–3 ha, and farmers generally divided the areas among a diversity of crops, so that different clusters of traps were often set out on land dedicated to different crops. Furthermore, some forest species only occurred at the deforested sites in those clusters that were closest to continuous forest, forest fragments or shade coffee while open habitat specialists avoided such areas. Forested areas were more homogeneous at the large scale. However, at the scale of clusters (tens of metres) they were often heterogeneous, which may have influenced beetle flight behaviour and their success in locating certain dung pats.

## Species coexistence in forest and deforested habitat

The defining concept of the aggregation model of coexistence is $T_{xy}$, which is an index of the relative strengths of intra- and interspecific aggregation. $T_{xy} > 1$ indicates instability and a tendency for species to be lost from the system. There are two important assumptions underlying $T_{xy}$. The first is that the impact of competition is proportional to per capita resource requirements (Sevenster 1996, Wertheim *et al.* 2000). The present study ensures that this assumption is met by taking account of relative beetle biomass, which is directly related to resource use (Doube 1990, Horgan 2001). Also, pitfall traps indicate the scramble for resources among all dung beetle species, including dung-rollers that are not captured in other types of baited trap (Giller & Doube 1994, Horgan 2005b). Total relocation of the dung, dung decay, and contamination by flies of 25-ml dung pats, usually occur within 24 h after dung deposition (Horgan 2005a, b) so that the trapping period would have adequately detected encounters between competing beetles. The use of relatively small baits ensured that competition would have occurred even at low beetle densities. A second assumption of $T_{xy}$ is that aggregation directly results from competitor visits or colonization. $T_{xy}$ was originally developed for fruit fly larvae competing in decomposing fruits and assumes that females lay only one egg per patch visit. This condition is perhaps rarely met in flies (Wertheim *et al.* 2000). However, in the case of neotropical dung beetles colonizing small dung pats, competition is directly related to the biomass of each beetle colonizer since dung pre-emption (relocation of dung away from competitors) is proportional to beetle size.

Community-level $T_{xy}$ (or $T_{x,-x}$) has been related to community saturation and stability. When $T_{x,-x}$ has a value of less than 1, communities are open to invasion because they are under-saturated, whereas above 1, communities are unstable and species are likely to be lost (Krijger & Sevenster 2001, Wertheim *et al.* 2000). In the present study, $T_{x,-x}$ was related to dung beetle species richness and biomass at the sites, but only in the April–May trapping period. Deforested sites generally had fewer species and less beetle biomass so that the dung beetle communities were unsaturated and open to invaders as indicated by lower overall $T_{x,-x}$ at the sites. Meanwhile, $T_{x,-x}$ at forested sites generally approached a value of 1 indicating greater instability due to intense interspecific competition for resources. This suggests that there is a higher species turnover at the forest sites. Krijger & Sevenster (2001) showed the opposite trend in fruit fly communities on decaying fruit at six Panamanian sites. Furthermore, Woodcock *et al.* (2002) found no apparent relationship between species diversity (related to habitat quality) and mean $T_{xy}$ (analogous to $T_{x,-x}$) in carrion flies feeding on slug cadavers in a range of Scottish birch woodlands. However, no study has successfully distinguished between cause and effect in these relations, so that there is no clear indication of whether aggregation determines species richness or vice-versa. Differences between the results presented here and those of the above-mentioned studies may be due to the fact that dung beetles are mobile and compete in the adult stage while fly larvae cannot escape competition. High intraspecific aggregation appears to be sufficient to maintain diversity in fly communities (Krijger & Sevenster 2001, Wertheim *et al.* 2000), but is insufficient to explain coexistence in neotropical dung beetle communities. Other mechanisms, including resource partitioning and inter-scale movement (i.e. variations in the frequency and magnitude of short-distance movement between patches and clusters, and long-distance dispersal between sites), may play a larger role in maintaining dung beetle diversity compared to fly diversity. Dung beetles have been noted to partition resources along a series of dimensions including habitat, season, light intensity and food source (Hanski & Cambefort 1991a, 1991b).

## Conclusions

In this study, carried out in a tropical montane region of central Peru, dung pats in deforested habitat were colonized by fewer species and a lower biomass of beetles than pats in adjacent forest fragments or continuous forest. In both types of habitat (forest and deforested), beetles were aggregated at all spatial scales examined and during each sampling period. There was considerable variation in the intensity of intra- and interspecific aggregation in each habitat at different spatial scales and during different sampling periods. Variation was likely related to habitat heterogeneity, changing conditions at the sites and dispersal of beetles within and between sites over time. Analyses of aggregation patterns revealed that dung beetle assemblages in deforested areas were unsaturated with low species turnover, indicating low levels of interspecific competition, whereas species turnover in forest habitat was apparently high due to intense competition for dung. Contrary to predictions from the aggregation model of coexistence, $T_{x,-x}$ was generally highest (approaching a value of 1) for dung beetles at the most species-rich sites, indicating that interspecific aggregation was generally too weak relative to intraspecific aggregation to explain the high diversity of species in forest habitat. This suggests that, whereas aggregation may promote dung beetle coexistence in the region, its contribution is small, particularly in forest habitat. Other mechanisms, including resource partitioning and inter-scale movement, are likely to play a greater role in maintaining the diversity of dung beetle assemblages in the region. The results also suggest that a breakdown in the aggregation mechanism has not been responsible for the loss of species at the sites following deforestation.

## ACKNOWLEDGEMENTS

The author thanks O. Baca, J. Gallegos, H. Huaynarupay-Peinado, C. Jordan, P. Roman, S. Signori, the International Potato Centre (CIP-San Ramón) and the municipality of San Ramón for access to field sites; C. Torpoco for help with fieldwork; J. Santiesteban at the Museo de Historia Natural in Lima for holding voucher specimens; B. Gill, F. Génier and H. Howden for aid in beetle identification and J. Finn, G. Forbes, P. Giller, S. Heard, J. Loo, C. Lucarotti, G. Moreau, C. Paponnet-Cantat, Y. Pelletier, D. Quiring, M. Rodríguez, and anonymous reviewers for helpful comments that improved the manuscript. This work was supported by Agriculture and Agrifood Canada (Y. Pelletier) and a NSERC discovery grant to D. Quiring.

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**Appendix 1.** Calculation of aggregation indices.

| Index | Formula | Symbols | Source |
|---|---|---|---|
| Intraspecific aggregation | $J = v_x/m_x^2 - 1/m_x$ | $v_x$ = sample variance for species x; $m_x$ = mean number of species x per sample | Ives 1991; Sevenster 1996 |
| Interspecific aggregation | $C_{xy} = Cov_{xy}/m_x m_y$ | $Cov_{xy}$ = covariance between species x and y; $m_x$ = mean total biomass of species x per sample; $m_y$ = mean total biomass of species y (super species complex) per sample | Ives 1991; Sevenster 1996 |
| Relative effect of aggregation of y on x as condition for coexistence | $T_{xy} \equiv 1 + C_{xy}/1 + J_y < 1$ | $C_{xy}$ = interspecific aggregation of species x; $J_y$ = aggregation of the other species (super-species complex) | Sevenster 1996; Wertheim *et al.* 2000 |
| Community level J | $J_{x,-x} = \exp[1/s \sum_{x=1}^{s} \ln(J + 1)] - 1$ | s = the total number of species occurring in the traps; J = intraspecific aggregation | Krijger & Sevenster 2001 |
| Community level $C_{xy}$ | $C_{x,-x} = \exp[1/s \sum_{x=1}^{s} \ln(C_{xy} + 1)] - 1$ | s = the total number of species occurring in the traps; $C_{xy}$ = interspecific aggregation | Krijger & Sevenster 2001 |
| Community level $T_{xy}$ | $T_{x,-x} = \exp[1/s \sum_{x=1}^{s} \ln(T_{xy})]$ | s = the total number of species occurring in the traps; $T_{xy}$ = relative effect of aggregation of y on x | Krijger & Sevenster 2001 |