

# Influence of land use on the trophic niche overlap of dung beetles in the semideciduous Atlantic forest of Argentina

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**Abstract.** 1. The degradation and replacement of natural ecosystems affect species abundance, diversity and interspecific interaction through the modification of resource availability and environmental conditions. Land uses preserving the forest canopy show higher species richness and similarity to the native forest.

2. In this study, we explored changes in the trophic niche overlap of dung beetles between the native forest and different land uses in the semideciduous Atlantic forest, under the hypothesis that trophic niche overlap increases with species richness.

3. We sampled dung beetles in protected native forests and four land uses (pine plantations, agroforestry parklands, silvo-pastoral systems and open pastures), using seven potential food sources (monkey, feline, tapir and deer dung, decomposing fruit, decomposing fungi and carrion). The species richness of each habitat, the trophic niche overlap and the relation between both measures were analysed. Also, we explored species trophic preferences in each habitat to explain and discuss the results obtained in trophic niche overlap measures.

4. As expected, our results showed a positive relation between species richness and trophic niche overlap. Moreover, the addition of different resources in open habitats did not increase species richness, suggesting that resource availability may not be the main mechanism explaining the impoverished dung beetle community observed in open habitats. Other mechanisms, such as physiological restrictions, may play a role in limiting the use of these habitats. Studies on the mechanisms leading to the patterns of species abundance and diversity observed in land uses are necessary to propose management recommendations that increase the sustainability of open habitats.

**Key words.** Competition, ecological niche, forest habitats, pasture habitats, Scarabaeoidea.

## Introduction

The degradation and replacement of native ecosystems affect environmental conditions (e.g. microclimate, soil

structure) (Osberg *et al.*, 1994; Oliveira-Filho & Fontes, 2000; Broennimann *et al.*, 2012) and the spatial and temporal availability of resources for species (ecological niche) (Culot *et al.*, 2013). Studies performed with dung beetles have shown that forested ecosystems have greater heterogeneity of food sources than disturbed habitats (Culot *et al.*, 2013; Puker *et al.*, 2014). In contrast, the abundance of single resources tends to be greater in disturbed habitats, such as cattle pastures (Hanski &

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Cambefort, 1991c; Louzada & Carvalho e Silva, 2009; Bourg *et al.*, 2016). The magnitude of these changes in biotic and abiotic conditions caused by the replacement of natural habitats influences the natural patterns of species abundance and diversity (species richness and composition) (Halffter & Arellano, 2002; Andrade-Núñez & Aide, 2010; Tonelli *et al.*, 2017). In general, land uses preserving the structure and composition of native vegetation and environmental conditions are more suitable for native species (Zurita & Bellocq, 2012; Audino *et al.*, 2014; Gómez-Cifuentes *et al.*, 2017).

Due to the intensive interspecific competition occurring in highly diverse ecosystems (such as tropical and subtropical forests), all dimensions of the ecological niche are involved in the coexistence of species (Hutchinson, 1957). In particular, dung beetle assemblages exhibit differences in several axes of the ecological niche due to the interspecific competition in highly diverse assemblages (Peck & Forsyth, 1982; Hanski & Cambefort, 1991b; Verdú *et al.*, 2004), including: trophic preferences (Hanski & Cambefort, 1991c; Lumaret & Iborra, 1996; da Silva *et al.*, 2012), resource size, time of colonisation, food relocation behaviour (paracoprid, telecoprid or endocoprid) (Hanski & Cambefort, 1991c), nesting strategies (Chao *et al.*, 2013), seasonal and daily activity (Krell-Westerwalbesloh *et al.*, 2004; Hernández, 2012), endothermy, thermoregulation and thermal tolerance (Verdú *et al.*, 2006, 2007; Gimenez Gomez *et al.*, In press). The study of the interaction between pairs of species (in different ecological axes) in a community allows understanding the mechanisms of coexistence under the same environmental conditions (Sexton *et al.*, 2017). Regarding the trophic niche, dung beetles show different preferences, from species requiring specific resources (specialists or species with low trophic niche breadth) (Halffter & Matthews, 1966; Hanski & Cambefort, 1991c; Bogoni & Hernandez, 2014) to species exploiting a large variety of resources (generalists or species with great trophic niche breadth) (Hanski & Cambefort, 1991c; da Silva *et al.*, 2012). The food resources used by dung beetles include mammal dung (Ratcliffe, 2013), carrion of vertebrates and invertebrates (Silveira *et al.*, 2006; Larsen *et al.*, 2009; Ratcliffe, 2013), and other decomposed products such as fungi, fruit and eggs (Halffter & Matthews, 1966; Navarrete-Heredia & Galindo-Miranda, 1997; da Silva & Bogoni, 2014). In general, all trophic resources exploited by dung beetles are ephemeral and heterogeneously distributed (Inward *et al.*, 2011), promoting interspecific competition and the differentiation of the ecological niche among species (Hanski & Cambefort, 1991c). Therefore, it is expected that a decrease in the heterogeneity, abundance and stability of resources (as a result of habitat disturbance) will result in a decrease in species diversity (both species richness and composition dissimilarity) and, consequently, in patterns of trophic niche overlap.

The Atlantic forest of Argentina, Brazil and Paraguay is one of the most diverse and threatened ecosystems worldwide (Di Bitetti *et al.*, 2003; Ribeiro *et al.*, 2009; Salomão & Iannuzzi, 2015). Previous studies in the

Atlantic forest have shown that the replacement of the native forest by different land uses affects the diversity and abundance of dung beetles (Peyras *et al.*, 2012; Hernández *et al.*, 2014; Gómez-Cifuentes *et al.*, 2017). While most studies with dung beetles describe changes in species diversity associated with forest replacement, little is known about the effect of environmental disturbance on the interaction among species. Consequently, in the present study, our objectives were as follows: (i) to evaluate how the trophic niche overlap of dung beetles differs among different habitats (native forest and four land uses) and (ii) to explore how changes in the trophic niche overlap of dung beetles and changes in species richness among habitats are related. Under the hypothesis that the trophic niche overlap of dung beetles increases with species richness, we expected that the land uses with higher species richness would have greater trophic niche overlap at the assemblage level. Furthermore, to gain insights into the possible interactions between dung beetle species (such as competition), we analysed trophic preferences of species, using multivariate analyses.

## Materials and methods

### Study area

The study was performed in the semideciduous Atlantic forest of Argentina (Fig. 1). The region is characterised by a warm climate and no dry season, with annual temperatures between 17 and 22 °C and an average annual rainfall of 2000 mm (Oliveira-Filho & Fontes, 2000). Landscapes in the study area comprise large remnants of continuous native forest in protected areas (Parque Nacional Iguazú and Parque Provincial Urugua-í, among others), tree plantations (mainly *Pinus taeda*), cattle pastures, 'yerba mate' plantations (*Ilex paraguariensis*) and small-scale annual crops (corn and tobacco, among others) (Zurita & Bellocq, 2012).

Dung beetles were sampled during the 2014 spring, the time of the year with the highest activity of dung beetles in the region (Hernández & Vaz-de-Mello, 2009; da Silva *et al.*, 2013). Within the study area, five replicates of native forest (Parque Nacional Iguazú and Parque Provincial Urugua-í) and four different land uses: (i) Mature pine plantations (10–12 years) (*Pinus taeda*); (ii) Native forest with livestock (agroforestry parklands); (iii) Pine plantations (*Pinus taeda*) with livestock (silvo-pastoral systems); and (iv) Deforested areas with livestock (open pastures), were selected. The land uses were selected based on previous studies showing that land uses preserving canopy cover (agroforestry parklands, pine plantations and the silvo-pastoral system) have greater richness and similarity in dung beetle species composition to the native forest than open pastures (Nichols *et al.*, 2007; Peyras *et al.*, 2012; Gómez-Cifuentes *et al.*, 2017). A detailed description of the selected land uses and the native forest can be found in Table S1. The land uses and the native forest

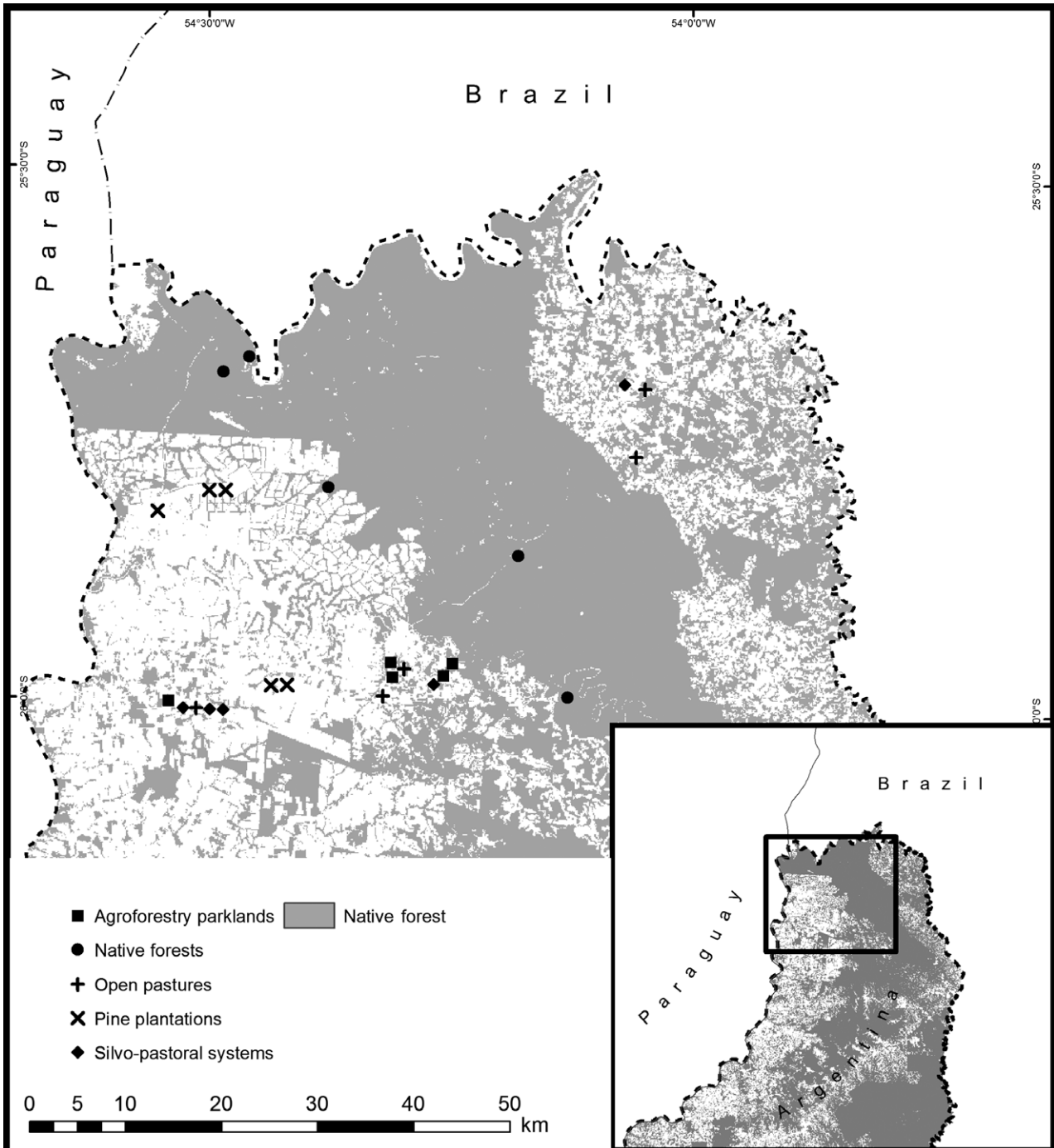


Fig. 1. Study area in the semideciduous Atlantic forest of Argentina.

were represented in four locations separated by more than 30 km (Esperanza Centro, Gobernador Lanusse, Andre-sito and Puerto Iguazú), reducing the potential influence of spatial autocorrelation within replicates of the same land use. In each locality, sites of the same land use were separated by at least 1 km to guarantee independence during the sampling period (da Silva & Hernández, 2015).

#### Dung beetle sampling

A grid of 150 m × 150 m was established in each sam-pling site (25 in total, five in the native forest and five in each land use). Each grid contained 16 traps separated by 50 m, to minimize interference between traps (16 traps × 25 sites = 400 traps) (Larsen & Forsyth, 2005;

Tshikae *et al.*, 2013). Traps consisted of a plastic container (12 cm in diameter and depth) filled with a 30% propylene glycol solution to avoid decomposition of individuals, without interfering with attraction (Nichols *et al.*, 2007). The 16 traps of each replicate were randomly baited with seven potential food resources of dung beetles (two traps per bait as subsamples): (i) dung from feline (*Leopardus pardalis*), (ii) dung from brocket deer (*Mazama nana*), (iii) dung from lowland tapir (*Tapirus terrestris*), (iv) dung from monkeys (*Alouatta caraya* and *Sapajus cay*), (v) decomposing fruits (*Syagrus romanzoffiana* and *Chrysophyllum gonocarpum*), (vi) carrion of vertebrate (decaying chicken) and (vii) decomposing fungi (Ascomycetes and Basidiomycetes). In addition, two traps were not baited and used as controls. The carrion baits were extracted from the freezer 12 h before being placed in the traps and the final decomposition process occurred in the field during the 72-h sampling period. The dung from feline, brocket deer and monkey was obtained from a local animal rescue centre ('Guira oga'), whereas the dung from lowland tapir and both fruits and fungi were obtained from the field. Four sampling periods of 72 h (12 days) were carried out, collecting the material and renewing the bait in each period. Previous studies with dung beetles normally used sampling periods of 48 h (da Silva & Bogoni, 2014; da Silva & Hernández, 2016); however, in this study, due to the large distances among sites and the large number of traps (400 traps), we used 72 h. All samples were preserved in 70% alcohol until further processing and identification of specimens at genus or species levels using taxonomic guides and the assistance of specialists (F. Vaz-de-Mello). Collected individuals were deposited at the Scarabaeidae Collection of the Instituto de Biología Subtropical – Iguazú (IBSI Sca), Misiones, Argentina.

#### Data analysis

We used the estimator of the sample coverage calculated from the *iNEXT* software (Chao *et al.*, 2016) to evaluate the sampling coverage. At community level, we performed a non-parametric Kruskal–Wallis and post hoc comparison from the 'conover.test' R package to compare the species richness among land uses and the native forest (Dinno, 2017; R Core Team, 2017).

To reduce the effects of incidental captures in the trophic niche overlap analyses, we only included species with abundance equal to or higher than 0.5% of the total capture per habitat. To estimate trophic niche overlap, we calculated the Czekanowski index for each pair of species within the assemblages (Feinsinger *et al.*, 1981) using the *EcoSim 7.0* software (Gotelli & Entsminger, 2001):

$$O_{12} = O_{21} = 1.0 - 0.5 \sum_{i=1}^n |p_{1i} - p_{2i}|,$$

where  $O_{12}$  is the overlap of species 1 with species 2, and  $p_{1i}$  is the fraction of observations for species 1 that

occurred in resource  $i$  in each replicate. The index ranges from zero to one, being zero pairs of species differing completely in resource preferences and one pairs of species fully overlapping in resource preferences. We first measured trophic niche overlap between all pairs of species for each replicate and then averaged all pairs to obtain a single value at the assemblage level for each replicate. Finally, we compared 'assemblage niche overlap' between land uses and the native forest, using the non-parametric Kruskal–Wallis test and post hoc comparison from the 'conover.test', R package (Dinno, 2017; R Development Core Team, 2017). In addition, to obtain a direct relation between species richness and niche overlap, we performed a generalised linear mixed model (GLMM) with 'habitat' (land uses and native forest) and 'site' (replicates) nested within 'habitat' as random effects, and species richness as a fixed effect from the 'nlme' R package (R Development Core Team, 2017; Pinheiro *et al.*, 2018). We tested the normality using the Shapiro test.

Finally, to explore the trophic preferences of individual species in each habitat (land uses and native forest), we performed a factorial correspondence analysis using the relative frequency of capture of each species on each bait (trophic preferences) (*PAST 2.16*; Hammer *et al.*, 2001). Additionally, we performed a cluster analysis, using trophic niche overlap between pairs of species in each habitat (*PRIMER 6*; Clarke & Gorley, 2006) (the trophic niche overlap for each pair of species was measured using the Czekanowski index explained previously).

## Results

#### Data quality, sampling efficiency and species richness

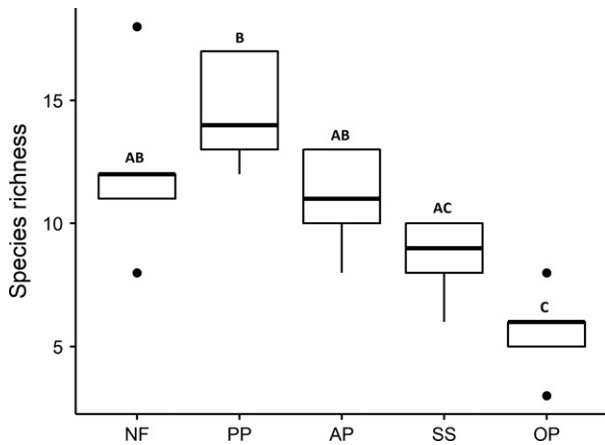
We collected 7393 individuals corresponding to 44 species, 26 of which were captured in the native forest, 25 in the pine plantations, 18 in the agroforestry parklands, 17 in the silvopastoral systems and 11 in the open pastures (see Table S2). The sampling effort captured more than 95% of species in all the habitats studied (see Table S3).

When comparing species richness, we found significant differences between habitats (K–W,  $H = 16.84$ ,  $n = 5$ ,  $P = 0.0019$ ). The native forest, pine plantations and agroforestry parklands showed higher and similar richness than open pastures, while silvopastoral systems represented an intermediate situation (Fig. 2).

#### Trophic niche overlap analysis at assemblage level

After excluding species with abundance lower than 0.5% per habitat, we included 18 species in the trophic niche overlap analyses (Table S2). Similar to that found for species richness, the trophic niche overlap differed between habitats (K–W,  $H = 17.82$ ,  $n = 5$ ,  $P < 0.005$ ) (Fig. 3; see Table S4). Agroforestry parklands and silvopastoral systems showed similar and higher trophic





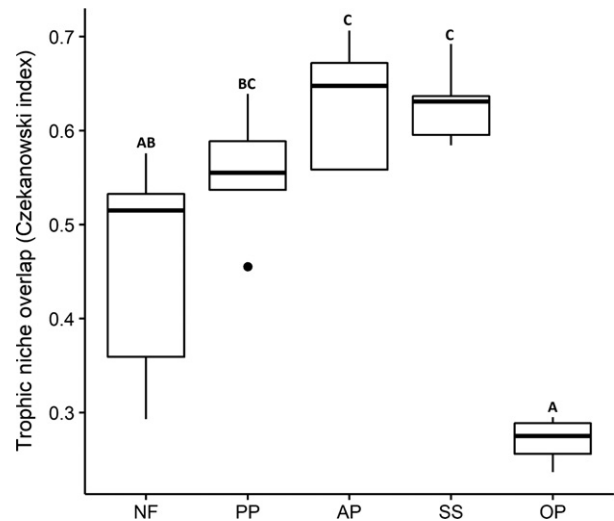
**Fig. 2.** Species richness of dung beetles (whiskers, median and outliers) in the native forest (NF) and four land uses (PP, pine plantations; AP, agroforestry parklands; SS, silvopastoral systems; and OP, open pastures) in the semideciduous Atlantic forest of Argentina. Different letters indicate significant differences with  $P < 0.05$  (Conover test, Kruskal–Wallis).

niche overlap than open pastures, while the native forest and pine plantations represented an intermediate situation. Finally, the GLMM (considering habitats and sites nested within habitat as random factors) showed that the trophic niche overlap increased with species richness (d.f. = 19,  $t = 2.06$ ,  $P = 0.05$ ).

#### Trophic preference analysis and trophic niche overlap at species level

From an exploratory viewpoint, we observed different specific associations between dung beetle species and baits in each habitat (Fig. 4). Monkey dung was the most commonly selected bait, compared with the other dung baits, in almost all habitats. Carrion and decomposing fungi were also preferred baits, compared with other baits (decomposing fruits, lowland tapir dung, brocket deer dung and feline dung). Finally, decomposing fruits and feline dung were the trophic resources with the lowest preference.

The results of cluster analysis, based on trophic niche overlap, reinforced the bait-species association observed in the factorial correspondence analysis (Fig. 4). In the native forest, a strong trophic niche overlap (around 80% or higher) was observed between (i) *Deltochilum morbillosum* Burmeister and *Canthon quinquemaculatus* Castelnau (species associated with carrion, feline dung and decomposing fungi), (ii) *Deltochilum* aff. *komareki* Balthasar and *Coprophanaeus saphirinus* (Sturm) (associated with carrion and decomposing fungi) and (iii) *Uroxys* sp. 1 and *Eurysternus caribaeus* (Herbst) (associated with lowland tapir dung). In pine plantations, a high trophic niche overlap (around 80% or higher) was observed between (i) *Coprophanaeus cyanescens* (Olsoufieff) and *C. quinquemaculatus*



**Fig. 3.** Dung beetle trophic niche overlap (whiskers, median and outliers) in the native forest (NF) and four land uses (PP, pines plantations; AP, agroforestry parklands; SS, silvopastoral systems; and OP, open pastures) in the semideciduous Atlantic forest of Argentina. Different letters indicate significant differences with  $P < 0.05$  (Conover test, Kruskal–Wallis).

(associated with carrion and brocket deer dung), (ii) *Dichotomius sericeus* (Harold), *Canthon conformis* (Harold) and *Uroxys thoracalis* Balthasar (associated with decomposing fungi and lowland tapir dung) and (iii) *D.* aff. *komareki* and *C. saphirinus* (associated with decomposing fungi). In agroforestry systems, three strong trophic overlap cases (>80%) were observed between: (i) *Eurysternus parallelus* Castelnau and *E. caribaeus* (associated with monkey dung), (ii) *C. saphirinus* and *C. cyanescens* (associated with decomposing fungi) and (iii) *Canthon histrio* (Lepelletier & Serville) and *C. conformis* (with no clear association with specific baits in this habitat). In silvopastoral systems, only a group formed by *C. saphirinus*, *C. quinquemaculatus* and *C. conformis* (associated with carrion and brocket deer dung) exhibited a high trophic niche overlap (>80%). Finally, in open pastures, a group formed by *C. cyanescens*, *C. quinquemaculatus* and *Eutrichillum hirsutum* (Boucomont) showed a high trophic niche overlap (>80%) (associated with carrion).

## Discussion

### Species diversity, trophic niche overlap and habitat use at assemblage level

Under the hypothesis that trophic niche overlap increases with species richness due to interspecific competition (Peck & Forsyth, 1982; Hanski & Cambefort, 1991a), we expected that land uses with higher species richness would have greater trophic niche overlap at the



assemblage level. The results found support our hypothesis: habitats with higher number of species (native forest, pine plantations, agroforestry parklands and silvo-pastoral systems) showed greater trophic niche overlap than open pastures. Also, reinforcing our hypothesis, we found a positive relation between niche trophic overlap and dung beetle richness.

A large number of studies have shown that the replacement, fragmentation and degradation of tropical and subtropical forests by intensive and semi-intensive land use (e.g. cattle raising, tree plantations and agriculture) may change the species richness and composition of dung beetles (Scheffler, 2005; Nichols *et al.*, 2007; Audino *et al.*, 2014; Gómez-Cifuentes *et al.*, 2017). However, these changes depend on the degree of conservation of the resources and condition of the original habitat (Nichols *et al.*, 2007; Hernández *et al.*, 2014; Gómez-Cifuentes *et al.*, 2017). In our study, land uses preserving forest canopy cover preserved not only forest species richness but also trophic niche overlap; in contrast, the open habitats showed reduced species richness and trophic niche overlap. To our knowledge, this is the first study that associates anthropic disturbance with changes in the trophic niche overlap in dung beetles. In previous studies, the anthropic disturbance has been associated with changes in daily activity (Daily & Ehrlich, 1996; Larsen, 2011), body size (Larsen *et al.*, 2005; Gardner *et al.*, 2008) and nesting strategy (Nichols *et al.*, 2013) in dung beetles, but never with changes in trophic preferences and trophic niche overlap. Also, previous studies have evaluated the trophic preferences of dung beetle species in the same habitat (Bustos-Gómez & Lopera Toro, 2003; Bogoni & Hernandez, 2014; Salomão *et al.*, 2017) but this is the first study comparing different habitats.

The degradation and replacement of natural habitats impose new environmental filters to native species (Mouillot *et al.*, 2013) through the modification of the available resources and environmental conditions (Osberg *et al.*, 1994; Oliveira-Filho & Fontes, 2000; Broennimann *et al.*, 2012). In the particular case of dung beetles, previous studies have shown that native forests have greater heterogeneity of ephemeral resources and that some land uses (e.g. open pastures) offer lower heterogeneity of resources but with greater abundance and stability (Hanski & Cambefort, 1991c; Louzada & Carvalho e Silva, 2009; Bourg *et al.*, 2016). The low number of species in open pastures recorded in this study and previous studies (Audino *et al.*, 2014; Menegaz *et al.*, 2015; Gómez-Cifuentes *et al.*, 2017) could be a consequence of this lower heterogeneity of available resources. However, in our study, the addition of greater resource diversity did not increase the number of species, suggesting that a different mechanism, such as

physiological restrictions, is limiting the use of open habitats in the region (V.C. Gimenez Gomez, J.R. Verdu, G.A. Zurita, unpublished data). This idea is supported by previous studies, suggesting that dung beetles of tropical and subtropical forests are sensitive to microclimate changes due to physiological restrictions (Sowig & Wassmer, 1994). In summary, our results suggest the idea that, in the semideciduous Atlantic forest, anthropogenic open habitats have an impoverished dung beetle assemblage, probably due to their low tolerance to extreme climate conditions and not to resource availability.

#### *Trophic preference and trophic niche overlap at species level*

Monkey dung was preferred by species that use dung as food source in almost all habitats (except open pastures). This is consistent with previous studies showing that, in the Neotropical region, dung beetles prefer dung from omnivorous mammals rather than from carnivorous or herbivorous mammals (Fincher *et al.*, 1970; Filgueiras *et al.*, 2009; Marsh *et al.*, 2013). These results suggest that the excrement of omnivorous mammals is potentially of better quality than other kinds of dung (Cambefort & Hanski, 1991; Hanski & Cambefort, 1991b). Due to habituation processes, we expected that species that use dung as food source in cattle systems (agroforestry parklands, silvopastoral systems and open pastures) were attracted to dung from herbivorous animals (lowland tapir or brocket deer) since the most abundant resource in this habitat is cow dung. However, our results showed that these species were more attracted to monkey dung in agroforestry parklands and silvopastoral systems and to feline dung in open pastures, suggesting a strong phylogenetic component on resource selection and a low influence of the habituation processes. Species that use decomposing material as food source showed similar preference to carrion and decomposing fungi. Dung beetles tend to be relatively generalists, so they can use different resources even where they still have a preference for a specific food item. In this case, they used two resources equally, although carrion was probably the most preferred (necrophagous species). Also, this result could be due to the similarity in the compounds and organisms that participate in the decomposition of both resources and to the fact that they are the main food sources for dung beetles (Anduaga & Halffter, 1993; Bustos-Gómez & Lopera Toro, 2003; Schmitte *et al.*, 2004). Finally, the low preference for decomposing fruit is not surprising since only few Neotropical forest dung beetles make use of this resource, compared to the preference for other resources (Halffter & Halffter, 2009; da Silva *et al.*, 2012; Salomão *et al.*, 2017).

**Fig. 4.** Factorial correspondence analyses based on dung beetle trophic preferences and cluster analyses based on trophic niche overlap in native forests and four land uses in the semideciduous Atlantic forest of Argentina. Numbers in the upper figure correspond to the baits used: (1) control, (2) carrion, (3) decomposing fruits, (4) wild feline dung, (5) decomposing fungi, (6) monkey dung, (7) brocket deer dung and (8) lowland tapir dung.

Differentiation in other ecological niche axes could probably explain the coexistence of species with high trophic niche overlap within the same habitat and reduce the interspecific competence (Paine *et al.*, 1981; Hanski & Cambefort, 1991b; Hernández *et al.*, 2009). As an example, both *Deltochilum* aff. *komareki* and *Coprophanæus saphirinus* preferred carrion and decomposing fungi, but *D.* aff. *komareki* is a nocturnal species and *C. saphirinus* is a diurnal species. A similar mechanism could explain the coexistence of *C. saphirinus* and *C. cyanescens* in agroforestry parklands; both species presented high preference for carrion but have different daily activity (*C. saphirinus* is a diurnal species and *C. cyanescens* is a nocturnal species). In these cases, the daily activity is the other ecological niche axis that could explain that species with the same trophic preference coexist in the same habitat. But, in other cases, we found some species that overlap in more than two ecological niche axes and, despite this, they coexist. For example, in the silvopastoral system, both *Canthon conformis* and *C. quinquemaculatus*, which belong to the same genus, preferred decomposing food, and are diurnal and telecoprid. The silvopastoral system is one of the habitats with lower species richness and therefore one may think that the dung beetle community is not saturated and that the trophic resources preferred by these species are sufficient to allow their coexistence. This would support the idea that food availability is not a limiting factor in highly disturbed habitats.

#### *Land use and mechanisms of species response*

The increase in habitat aptitude of land uses for native biodiversity is a priority in the development of production systems with greater environmental sustainability (Donald, 2004; Cowie *et al.*, 2011). Although describing changes in species diversity and abundance associated with native habitat replacement is necessary, a more detailed understanding of the ecological and physiological mechanisms behind the response of species and communities to disturbance will improve land use management for conservation purposes. Our results suggest that trophic resource availability may not be a primary limitation for dung beetle use of land uses in the semideciduous Atlantic forest. Other mechanisms, such as physiological restrictions, may be more important determining the ability of species to exploit human-created habitats. In this regard, Alves *et al.* (In press) have recently studied the elytra spectrophotometric response of Neotropical dung beetles to three types of radiation, in two types of habitats. They found no differences between species that use a specific habitat; only species inhabiting both habitats showed a different pattern. Species inhabiting both habitats have the advantage that they can avoid overheating in open areas (with more solar radiation) through the expulsion of internal body heat. In open areas, they may be favored by protection against predation due to their bee-like coloration pattern. Although this is a relevant study on the

ecophysiology of dung beetles, more studies in this approach are needed to better understand the effects of the disturbance and propose management recommendations that increase the sustainability of anthropogenic landscapes.

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#### **Supporting Information**

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12299:

**Table S1.** Description of the native forest and the land uses selected in the semideciduous Atlantic forest of Argentina.

**Table S2.** Number of individuals captured in the native forest (NF) and the four land uses selected (PP, pine plantations; AP, agroforestry parklands; SS, silvopastoral systems; OP, open pastures) in the semideciduous Atlantic forest of Argentina.

**Table S3.** Sampling coverage results for each of the habitats studied in the semideciduous Atlantic forest of Argentina. NF, native forests; PP, pine plantations; AP, agroforestry parklands; SS, silvopastoral systems; OP, open pastures.

**Table S4.** Czekanowski index of trophic niche overlap of dung beetles in the native forest and four land uses selected in the semideciduous Atlantic forest of Argentina.

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