

# Are there pitfalls to pitfalls? Dung beetle sampling in French Guiana

Dana L. Price · Francois Feer

Received: 6 October 2011 / Accepted: 15 August 2012 / Published online: 4 September 2012  
© Gesellschaft für Biologische Systematik 2012

**Abstract** Dung beetles have widely been accepted as cost-effective indicator taxa for biodiversity assessment; thus, standard protocols have been created to examine their species richness and diversity in many habitats. However, the vast majority of studies adopt short-term sampling protocols; few studies have quantified sampling efficiency at longer time scales or tested the efficacy of species richness estimates. Here we present long- and short-term sampling data from two regions of French Guiana: the Nouragues Tropical Forest Research Station and Kaw Mountain. We examine species richness and diversity, and use these data to make suggestions for future biodiversity assessments of dung beetles using dung baited pitfall transects. Species richness estimates based on short-term samples strongly underestimate the actual species richness by approximately 40 %. Duration of trapping was found to be more important than the number of traps and length of transects; by setting a second transect (4-day sample period) in the same habitat of Nouragues, thereby increasing the sample duration, the number of species increased by 14 %.

**Keywords** Dung beetles · Bioindicator · Nouragues · Kaw Mountain · Species richness · Species diversity

## Introduction

Dung beetles (Coleoptera: Scarabaeidae) are both economically and ecologically important insects. Their role in the burial of dung is essential to its decomposition and therefore recycling of nutrients into the soil, reduction of dung-breeding parasites and secondary seed dispersal (Nichols et al. 2008). The Scarabaeines in particular have repeatedly been used for assessing and monitoring biodiversity and are frequently used as a model group for understanding broad biodiversity trends (Spector 2006). In addition, Gardner et al. (2008) have identified dung beetles and birds as being especially cost efficient for evaluating and monitoring the ecological consequences of habitat change.

The development of indicators has become an increasingly common approach to meet the need for assessment tools. An indicator taxon is one variable that supplies information about other variables in the environment. These variables are difficult to assess (Bockstaller and Girardin 2003); however, they may provide early warning of ecological changes such as habitat disturbances, particular resource decreases and their functional consequences on the ecosystems. However, there are very few studies that provide the baseline data needed to assess individual methods of sampling for a given indicator taxon. In a study to examine the effectiveness of two trapping methods, baited pitfall traps and flight intercept traps (FIT's), over a 2-year period in Borneo, Davis (2000) found that pitfall traps were capable of sampling approximately 80 % of the dung beetle species in that region. In biodiversity assessments, often conducted in a short period of time or single, once-off assessments (McGeoch et al. 1998) and with limited funding (Gardner et al. 2008), the aim is comparing several sites or monitoring the same site at different periods. Trapping with human dung bait reveals itself to be the best sampling method in many tropical forests (Larsen et al. 2006). At least in the

This is a contribution to the Festschrift for Michael L. May

D. L. Price (✉)  
Department of Biological Sciences, Salisbury University,  
1101 Camden Avenue,  
Salisbury, MD 21801, USA  
e-mail: dlprice@salisbury.edu

F. Feer  
Laboratoire d' Ecologie, Muséum National d'Histoire Naturelle,  
CNRS UMR 7179,  
4 avenue du Petit Château,  
91800, Brunoy, France  
e-mail: feer@mnhn.fr

Neotropics, most of the coprophagous beetles are captured by this method, but the question is what the number of species collected with a short assessment indicates concerning the total diversity obtainable with the same method on the same site.

Thorough studies regarding the species composition, flight activity and ecological segregation of dung beetles in the Les Nouragues Tropical Forest Research Station of French Guiana have been conducted for over 15 years (Feer 2000; Feer and Pincebourde 2005; Feer unpublished data). Additional studies of the dung beetle fauna of French Guiana (Gillett, personal communication, 2010) as well as further studies of Nouragues and Kaw are underway. Here we present data regarding the biodiversity of dung beetles (Scarabaeinae) attracted to ground baited pitfall traps using a single, once off assessment in both Nouragues and Kaw Mountain. The main objective of this article was to examine the effectiveness of using a single standardized protocol for the collection of dung beetles in French Guiana where long-term data are available. We discuss species richness and diversity measures and hope to provide stricter guidelines for future assessment of dung beetle biological diversity.

## Materials and methods

### Study sites

French Guiana includes some of the largest tracts of intact rainforest in the Amazon region (Feer 2000). This research deals with the sampling of dung beetles (Scarabaeidae: Scarabaeinae) in two locations of French Guiana. These include the Nouragues Research Station at the ‘inselberg’ site (N 04°05' W 52°40', altitude 100 m) on the Montagnes Balenfois massif 100 km south of Cayenne and the Amazon Nature Lodge (N 04°33' W 52°12', altitude 300 m), settled in the Mountains of Kaw near the Kaw Nature Reserve 45 km southeast of Cayenne. Nouragues (NRS) is situated in a 1,000-km<sup>2</sup> wilderness reserve consisting of undisturbed rainforest (Bongers et al. 2001). The rainforest in Kaw Mountain (KM) is locally disturbed by former logging, the road on the ridge and logging trails (Feer, personal observation). The fauna of large vertebrates in Kaw is less abundant and diverse than in the Nouragues area because of moderate hunting pressure (Thoisy et al. 2005).

*Long-term sampling protocols* Extensive sampling by the second author was conducted in the Nouragues Research Station from 1995–2010 using human baited pitfall traps. Sampling was performed using transects of 450 m with ten pitfall traps set every 50 m. The majority of the collections were made over a 4-day sample period with bait renewed after 2 days. A total of 21 4-day samples were collected, including

2 with only five traps. Traps consisted of plastic pots, 10 cm in diameter and 15 cm deep, buried in the ground and filled with a solution of water with detergent and sodium chloride. Traps were baited with human dung put in a plastic container suspended over the pot. Beetles were collected during the months of February–June and October–November.

Long-term sampling of Kaw Mountain was conducted from 2009–2011. Sampling was performed with 12 pitfall traps along a 300-m transect in order to increase the sample. Four sample periods of 4 days each were implemented. The site of collections at KM was considered to be a high forest most similar in composition and structure to Nouragues. Specimens were identified by comparison to collections in the Laboratoire d'écologie (Brunoy) and the Laboratoire d'entomologie of the Muséum national d'histoire naturelle (Paris) supervised by Yves Cambefort.

*Short-term sampling protocols* Short-term sampling of NRS and KM were conducted in 2005 in the same regions as mentioned above. Samples that were taken in different locations during the long-term study were regarded as different habitats and were discarded. Using standardized pitfall trap transects (Larsen and Forsyth 2005), five traps were baited with human dung and placed 50 m apart along a linear transect of 200 m in each site. Traps consisted of 16-oz. plastic “Solo” cups buried in the ground and filled with a small amount of non-toxic antifreeze. Traps were baited with human dung, which was wrapped in cheese cloth and suspended above the trap using a stick. Transects were set and samples were collected every 24 h for 4 days, with bait renewed after 2 days. This trapping method and period are usually adequate for sampling the majority of Alpha diversity (Spector and Forsyth 1998; Larsen and Forsyth 2005). Beetles were collected during the end of the rainy season from July 17–7 August 2005, with one transect sampled in KM in a mix of low forest and two sampled in NRS. Upon collection, samples were then transferred into 80 % ethanol. Samples were later sorted and counted for species diversity and abundance data. Specimens were pinned, labeled and identified to genus and species by Sacha Spector when possible. Voucher specimens were then sent to Bruce Gill (Ottawa, Canada) for positive species identifications. All vouchers are currently held at Salisbury University, Salisbury, MD, USA, in the personal collection of Dana L. Price.

### Data analyses

We used EstimateS 8.20 (Colwell 2009) to examine all data tabulated from short- and long-term studies of Scarabaeinae dung beetles. We examined the species richness and diversity among all three transects conducted during 2005. For comparison of long- and short-term sampling data, we estimated species richness using several nonparametric

**Table 1** Species diversity and abundance of dung beetles collected during a three-week expedition to French Guiana. T1KM: Transect 1 Kaw Mountain; T2NRS: Transect 2 Nouragues Research Station; T3NRS: Transect 3 Nouragues Research Station

Species name	T1KM	T2NRS	T3NRS
<i>Agamopus castaneus</i> Balthasar	0	0	3
<i>Ateuchus murrayi</i> (Harold)	7	8	7
<i>Ateuchus oblongus</i> GROUP	5	5	2
<i>Ateuchus simplex</i> (Audinet-Serville)	32	61	188
<i>Ateuchus</i> sp.	0	0	1
<i>Canthidium deyrollei</i> Harold	0	2	2
<i>Canthidium dohrni</i> Harold	0	2	10
<i>Canthidium gerstaeckeri</i> Harold	2	10	0
<i>Canthidium</i> sp. 1	3	0	2
<i>Canthidium</i> sp. 2	0	1	0
<i>Canthidium</i> sp. 3	5	13	17
<i>Canthidium</i> sp. 4	2	1	3
<i>Canthon bicolor</i> Laporte de Castelnau	14	76	45
<i>Canthon quadriguttatus</i> (Olivier)	3	0	1
<i>Canthon semiopacus</i> Harold	3	0	1
<i>Canthon sordidus</i> Harold	90	136	172
<i>Canthonella silphoides</i> (Harold)	1	1	0
<i>Deltochilum carinatum</i> Westwood	0	2	0
<i>Deltochilum diringshofeni</i> P. & M.	10	3	21
<i>Deltochilum icarus</i> (Olivier)	1	1	15
<i>Deltochilum septemstriatum</i> Paulian	1	3	4
<i>Dichotomius boreus</i> (Olivier)	2	29	14
<i>Dichotomius lucasi</i> (Harold)	0	12	13
<i>Dichotomius subaeneus</i> Laporte de Castelnau	5	3	3
<i>Dichotomius</i> sp.	0	1	0
<i>Eurysternus balachowskyi</i> H. & H.	11	17	20
<i>Eurysternus cambeforti</i> Genier	0	2	0
<i>Eurysternus caribaeus</i> (Herbst)	12	14	25
<i>Eurysternus cayennensis</i> Laporte de Castelnau	42	85	123
<i>Eurysternus foedus</i> Guérin-Meneville	3	0	2
<i>Eurysternus hamaticollis</i> Balthasar	1	0	0
<i>Eurysternus hypocrita</i> Balthasar	82	61	51
<i>Hansreia affinis</i> (Fabricius)	49	37	4
<i>Onthophagus clypeatus</i> Blanchard	2	11	15
<i>Onthophagus haematopus</i> Harold	13	64	26
<i>Onthophagus rubescens</i> Blanchard	86	107	86
<i>Oxysternon durantoni</i> Arnaud	6	16	7
<i>Oxysternon festivum</i> (Linnaeus)	2	12	12
<i>Phanaeus chalconelas</i> (Perty)	2	5	0
<i>Scybalocanthon pygidialis</i> (Schmidt)	2	11	5
<i>Sylvicanthon bridarollii</i> (Martinez)	42	11	3
<i>Trichillum pauliani</i> Balthasar	0	13	1
<i>Uroxys</i> sp.	5	83	18

estimators, including Chao1 (Chao 1984; Colwell and Coddington 1994), ICE (Incidence-based Coverage Estimator) and ACE (Abundance-based Coverage Estimator) (Chazdon et al. 1998; Chao et al. 2000). Chao1 is based on the number of singletons and doubletons or rare species in a sample. The

ACE is based on species with abundances between 1 and 10 individuals, and the estimate is completed with the addition of species with numbers greater than 10, where ICE focuses mainly on species found with  $\leq 10$  individuals (Magurran 2004). Species accumulation curves were used for short-

term data to illustrate the rate at which new species are sampled. Colwell and Coddington (1994) argue that species accumulation curves are more informative when samples are taken in a systematic way, as we have done here using standardized sampling techniques. Magurran (2004), however, reports that if the study is not exhaustive, the curves will not directly reveal the total species richness.

Species diversity indices were determined using Fisher's alpha, Shannon diversity, exponential Shannon diversity and Simpson diversity (the reciprocal form). Fisher's alpha is meaningful when  $N > 1,000$ , and Simpson diversity provides a good estimate of diversity when only a small sample size is available (Magurran 2004; Colwell 2009). We used the Shannon index, which is one of the most commonly reported indices, and we used the exponential Shannon Diversity, which is meaningful because it provides the number of species that would have been found in the sample if all species had been equally common (Whittaker 1972; Magurran 2004). It should be mentioned, however, that these indices are most often used when comparing two different sites, not the same site. Here we are comparing long- with short-term data.

## Results

### Comparison of short-term sampling transects

A total of 43 species of dung beetles (Scarabaeinae) including 2,273 individuals were collected during a 3-week sample period (Table 1). Additional species collected but not included in these analyses include *Aphodius* sp. (Aphodiinae) and *Coloides* sp. (Hybosoridae). Thirty-three species were collected in Kaw Mountain (KM), while 36 and 35 were collected in Nouragues Research Station (NRS), respectively (Table 2). Overall, the species richness for the NRS was only slightly higher than that of the KM. However, abundance of individuals collected at the KM was just under 60 % of the total individuals collected in both transects two and three of the NRS. The Nouragues Research Station (second transect) produced the highest overall estimates for species richness and species diversity (Table 2). Species accumulation curves are similar among all three transects (Fig. 1).

### Comparison of long and short-term data

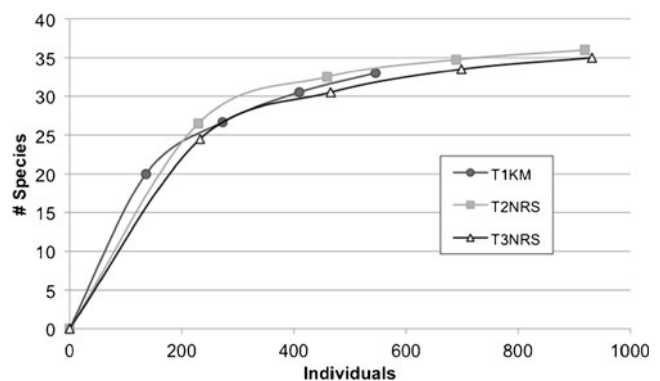
**Nouragues research station** Extensive dung beetle sampling from 1995–2010 using human feces baited pitfall traps produced a total of 78 species including 13,180 individuals (Table 3). From these data we determined that after just one sample period (4 days and 2 samples), 50 % of the dung beetles species (Scarabaeinae) were found, and 76 % of the species were found after eight samples (four sample periods of

**Table 2** Species richness and abundance of dung beetles for each transect from short-term sampling data. T1KM: Transect 1 Kaw Mountain; T2NRS: Transect 2 Nouragues Research Station; T3NRS: Transect 3 Nouragues Research Station

	T1KM	T2NRS	T3NRS
Species richness	33	36	35
Abundance	546	919	932
Estimated Species Richness			
Chao1	33.75	38	36.2
ICE	40.65	38.32	38.24
ACE	35.31	39.53	37
Species Diversity			
Fisher's alpha diversity index	7.72	7.47	7.18
Shannon diversity	2.4	2.69	2.47
Shannon exponential mean ( $e^H$ )	14.16	17.38	14.04
Simpson's index ( $1/D$ )	10.05	13.05	9.09

4 days each) (Fig. 2). There were 12 species sampled with only one or two individuals recorded during the 15-year trapping period. Estimated species richness from long-term data is 80 (Chao1), 81 (ACE) and 84 (ICE). The species accumulation curve is congruent with the species richness estimators, suggesting another three to five more species may be found in this region of French Guiana (Fig. 3). When all 21 samples from the long-term study were pooled for species richness, we found an average of 35 species sampled.

Short-term sampling of dung beetles during 2005 in the NRS found a total of 42 species and 1,851 individuals (Table 3). Similar to the above-mentioned study, 49 % of the dung beetles were found in just one 4-day sampling period. Estimated species richness was 45 (Chao1), 47 (ACE) and 46 (ICE). Overall, the species richness is immensely underestimated when using the described short-term sampling protocol. All species diversity indices for



**Fig. 1** Species accumulation curves from short-term dung beetle sampling in 2005. T1KM: Transect 1 Kaw Mountain; T2NRS: Transect 2 Nouragues Research Station; T3NRS: Transect 3 Nouragues Research Station

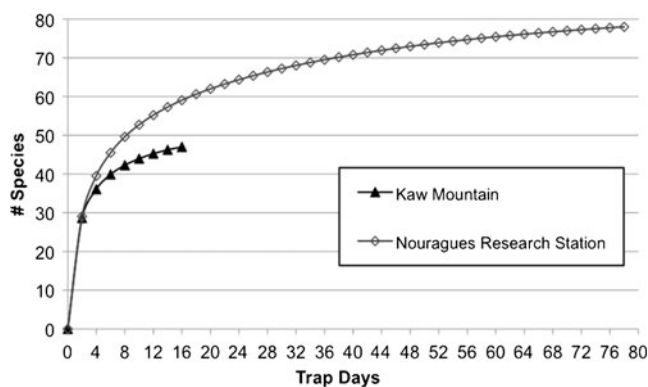
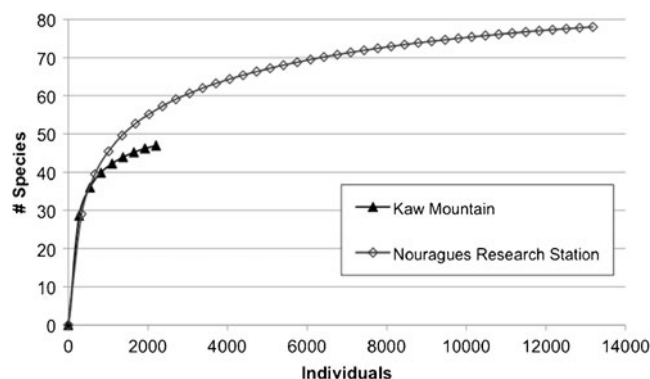
**Table 3** Comparison of the species richness and diversity of dung beetles sampled from the Nouragues Research Station. Data are shown from a long-term study conducted over 15 years, and a short term study conducted during two weeks

	Long term study	Short term study
Species richness	78	42
Abundance	13,180	1851
Species richness estimators		
Chao1	80.14	45
ICE	84.01	46.08
ACE	81.48	46.75
Species diversity measures		
Fishers's alpha diversity index	11.00	7.65
Shannon diversity	3.15	2.83
Shannon exponential mean ( $e^H$ )	23.26	16.9
Simpson's index (1/D)	15.20	11.67

long-term sampling were found to be higher than those of the short-term studies (Table 3).

**Kaw mountain** A total of 47 species and 2,202 individuals were sampled in Kaw Mountain from 2009-2011 (Table 4). The Chao1 (49), ICE (50) and ACE (50) all estimate much lower species richness for KM when compared to Nouragues Research Station. The species accumulation curve of the KM data also suggests a much lower asymptote than that of the NFS (Fig. 3). Diversity measures indicate high species diversity of 8.44 (Fisher's alpha index), 18.36 (Shannon's exponential mean) and 11.07 (Simpson's index).

Short-term sampling found 33 species and 546 individuals (Table 4). It should be noted that during the first 4-day sampling period of the long-term study found just 3 more species and 4 more individuals (36 species and 550 individuals) using a 300-m transect with 12 traps. Furthermore,

**Fig. 2** Species accumulation curves using species richness and trap days from an exhaustive dung beetle sampling study conducted in the Nouragues Research Station from 1995-2010, and a three-year dung beetle sampling study conducted in Kaw Mountain during 2009-2011**Fig. 3** Species accumulation curves using species richness and number of individuals from an exhaustive dung beetle sampling study conducted in the Nouragues Research Station from 1995-2010, and a three-year dung beetle sampling study conducted in Kaw Mountain during 2009-2011

when all four samples from the 2009-2011 study were examined for species richness, we found an average of 34 species sampled. Using the long-term sampling data presented for NRS, we can approximate finding 33-36 additional species in this region that have not been sampled. Overall, ICE (41) estimated the highest species richness for Kaw, with 82 % of the total species richness found in just one sample period. The Incidence-based Coverage Estimator potentially predicts a higher estimate than that of the Nouragues region based on the lower abundance of individuals trapped and most importantly the number of individuals found where less than ten individuals are recorded.

## Discussion

The data provided here are meant to provide more strenuous guidelines for the sampling of dung beetles for short, once

**Table 4** Comparison of the species richness and diversity of dung beetles sampled from Kaw Mountain. Data are shown from a 3-year study conducted from 2009-2011, and a short-term study during 2005

	3-year study	Short term study
Species richness	47	33
Abundance	2202	546
Species richness estimators		
Chao1	48.67	33.75
ICE	49.79	40.65
ACE	50.11	35.31
Species diversity measures		
Fishers's alpha diversity index	8.44	7.72
Shannon diversity	2.91	2.4
Shannon exponential mean ( $e^H$ )	18.36	14.16
Simpson's index (1/D)	11.07	10.05



off biodiversity assessments. We recommend that species richness estimators be used with caution and that emphasis should be placed on the overall dung beetle community structure where diversity measures of dung beetles can provide a valuable tool. Analysis of all 4-day samples (short and long-term) indicate species richness of short-term sampling methods using only pitfalls baited with human feces will produce ~50 % of the number of species found in a particular region. The long-term data suggest that ~70 % of the dung beetle species are present in the first 2,000 specimens, although new species are still recovered even after 10,000 specimens. Feer (2000) in a study of the dung and carrion beetle composition of Nouragues suggested that the number of species caught per day with ten or five traps is very similar, indicating that the number of traps is less important than the duration of trapping. Our data are congruent with these findings. Indeed, the same 4-day sample period with ten traps (long-term data) or five traps (short-term data) gave very similar numbers of species. The same can be said for the data collected from KM; using 12 traps instead of 5 and the same sampling period did not increase the species richness. On the other hand, by setting a second transect in the same type of habitat of NRS, which increased the sample duration, the number of species increased by 14 %.

Other short-term studies conducted with much longer transects, but similar 4-day sampling protocols in similar habitats give species richness with the same order of magnitude. Larsen (2007) found 33 and 24 species in Lely and Nassau Plateaus, Suriname. Most recently in a Rapid Assessment Program to examine the dung beetles of the Kwamalasamutu Region, Larsen (2011) reported collecting 45, 49 and 47 species at three sites. In both studies mentioned above, ten traps were set 150 m apart along a linear transect. We observed that species richness in KM, measured with the same sampling protocol and effort, was slightly smaller than in NRS. The difference became more pronounced when an additional 4-day sample was conducted in NRS. Knowing only the short-term data, we would be unable to make valuable assumptions upon the origin of the difference.

One factor that may contribute to biased species diversity is sampling only during either the wet or dry season in the tropics. In a study of temporal variations of the diversity and abundance of copro-necropagous dung beetles on a 1-year cycle near PetitSaut dam (French Guiana), Feer and Cerdan (2006) found maxima in the dry season and in the rainy season. Fluctuations reach 30–56 % with no correlation with pluviometry. Fourteen of the most abundant species, however, were present all year round. Larsen (Pers. comm. 2010) suggests that out of about 200 species in the SW Amazon and on the Osa Peninsula of Costa Rica, there are only a few species sampled in only one season. Abundance,

however, fluctuates quite strongly depending on the weather, but species seem to be present year round. These findings are also evident in our research with dung beetles sampled from NRS. One must, however, be cautious when sampling in an area with a relatively pronounced dry period (Feer and Cerdan 2006 and references therein). Marked variations have been observed in tropical areas where the dry season is long and intense; few or no dung beetles were present outside the rainy periods (Janzen 1983; Andresen 2005).

Clear differences in species richness appeared between Kaw and Nouragues long-term data with only 2,000 specimens in both samples. Lower richness in KM is predicted by the lower resource level related to the impoverished vertebrate fauna (Andresen and Laurance 2007; Nichols et al. 2009) and disturbance of the forest structure by logging (Feer 2008; Nichols et al. 2007). The same difference was shown with short-term data, but uncertainty remained. Accordance with the long-term data may be related to the correlated seasonal variations in the Kaw and Nouragues areas. Dung beetles have repeatedly demonstrated their usefulness as a focal taxon in biodiversity studies (Larsen and Forsyth 2005; Spector 2006; Larsen 2011). Our recommendation here is to carefully consider short-term sampling in tropical forests, especially when high variations of pluviometry occur. To maximize the length of the sampling period during an assessment or to repeat the assessment at different periods of the year remains the best way to enhance the representativeness of short-term data.

**Acknowledgements** The short-term sampling for this research would not have been possible without the funding and encouraging support provided by Michael L. May. He has been an advisor, mentor and friend, and he is a genuinely nice person. Collections in 2005 were also part of a Smithsonian Institute expedition to sample the ants of French Guiana in collaboration with Ted Schultz and John LaPolla. We thank Trond Larsen for his review and comments on this manuscript. We also thank Sacha Spector and Bruce Gill for their time with identification of specimens.

## References

- Andresen, E. (2005). Effects of season and vegetation type on community organization of dung beetles in a tropical dry forest. *Biotropica*, 37(2), 291–300.
- Andresen, E., & Laurance, S. G. (2007). Possible direct effects of mammal hunting on dung beetle assemblages in Panama. *Biotropica*, 39, 141–146.
- Bockstaller, C., & Girardin, P. (2003). How to validate environmental indicators. *Agricultural Systems*, 76, 639–653.
- Bongers, F., Charles-Dominique, P., Forget, P.-M., Théry, M. (2001). Nouragues dynamics and plant-animal interactions in a neotropical rainforest. (Eds.) (p. 421). Dordrecht: Kluwer Academic Publishers.
- Chao, A. (1984). Non-parametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics*, 11, 265–270.

- Chao, A., Hwang, W.-H., Chen, Y.-C., & Kuo, C.-Y. (2000). Estimating the number of shared species in two communities. *Statistica Sinica*, 10, 227–246.
- Chazdon, R. L., Colwell, R. K., Denslow, J. S., & Guariguata, M. R. (1998). Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica. In F. Dallmeier & J. A. Comiskey (Eds.), *Forest biodiversity research, monitoring and modeling: Conceptual background and Old World case studies* (pp. 285–309). Paris: Parthenon Publishing.
- Colwell, R.K. (2009). EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.2. User's Guide and application published at: <http://purl.oclc.org/estimates>.
- Colwell, R. K., & Coddington, J. A. (1994). Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society (Series B)*, 345, 101–118.
- Davis, A. J. (2000). Species richness of dung-feeding beetles (Coleoptera: Aphodiidae, Scarabaeidae, Hybosoridae) in tropical rainforest at Danum Valley, Sabah, Malaysia. *The Coleopterists Bulletin*, 54(2), 221–231.
- de Thoisy, B., Renoux, F., & Julliot, C. (2005). Hunting in northern French Guiana and its impact on primate communities. *Oryx*, 39, 1–9.
- Feer, F. (2000). Dung and carrion beetles (Scarabaeidae s. str. et Aphodiidae) of the rain forest of French Guiana: species composition and structure of populations. *Annales de la Société Entomologique de France*, 36(1), 29–43.
- Feer, F. (2008). Responses of dung beetle assemblage to characteristics of rain forest edges. *Ecotropica*, 14, 49–62.
- Feer, F., & Cerdan, P. (2006). Variations saisonnières d'activité dans un assemblage de Coléoptères nécrophages (Coleoptera, Scarabaeidae) en forêt tropicale humide. *Revue d'Écologie (Terre Vie)*, 61, 247–260.
- Feer, F., & Pincebourde, S. (2005). Diel flight activity and ecological segregation within an assemblage of tropical forest dung and carrion beetles. *Journal of Tropical Ecology*, 21(1), 21–30.
- Gardner, T. A., Barlow, J., Araujo, I. S., Avila-Pires, T. C., Bonaldo, A. B., Costa, J. E., Espósito, M. C., Ferreira, L. V., Hawes, J., Hernandez, M. I. M., Hoogmoed, M. S., Leite, R. N., Lo-Man-Hung, N. F., Malcolm, J. R., Martins, M. B., Mestre, L. A. M., Miranda-Santos, R., Overal, W. L., Parry, L., Peters, S. L., Ribeiro, M. A., da Silva, M. N. F., Motta, C. D. S., & Peres, C. A. (2008). The cost-effectiveness of biodiversity surveys in tropical forests. *Ecology Letters*, 11, 139–150.
- Janzen, D. (1983). Seasonal change in abundance of large nocturnal dung beetles (Scarabaeidae) in a Costa Rican deciduous forest and adjacent horse pasture. *Oikos*, 41(2), 274–283.
- Larsen, T.H. (2007). Dung beetles. A rapid biological assessment of the Lely and Nassau Plateaus, Suriname. RAP Bulletin of Biological Assessment 43. Arlington, VA: Conservation International. (pp 99–101).
- Larsen, T. H. (2011). Dung beetles. A rapid biological assessment of the Kwamalasamutu Region, Southwestern Suriname. *RAP Bulletin of Biological Assessment*, 63, 91–103.
- Larsen, T. H., & Forsyth, A. (2005). Trap spacing and transect design for dung beetle biodiversity studies. *Biotropica*, 37, 322–325.
- Larsen, T. H., Lopera, A., & Forsyth, A. (2006). Extreme trophic and habitat specialization by Peruvian dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *The Coleopterists Bulletin*, 60, 315–324.
- Magurran, A. E. (2004). *Measuring biological diversity* (p. 256). Oxford: Blackwell Publishing.
- McGeoch, M. M. (1998). The selection, testing and application of terrestrial insects as bioindicators. *Biological Reviews*, 73, 181–201.
- Nichols, E., Larsen, T., Spector, S., Davis, A. L., Escobar, F., Favila, M., Vulinec, K., & The Scarabaeinae Research Network. (2007). Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. *Biological Conservation*, 137, 1–19.
- Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezcuita, S. A., & Favila, M. E. (2008). Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation*, 141, 1461–1474.
- Nichols, E., Gardner, T. A., Peres, C. A., Spector, S., & The Scarabaeinae Research Network. (2009). Co-declining mammals and dung beetles: an impending ecological cascade. *Oikos*, 118, 481–487.
- Spector, S. (2006). Scarabaeine dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation. *The Coleopterists Bulletin*, 60, 71–83.
- Spector, S., & Forsyth, A. B. (1998). Indicator taxa in the vanishing tropics. In A. Balmford & G. Mace (Eds.), *Conservation in a changing world* (pp. 181–210). London: Zoological Society of London.
- Whittaker, R. H. (1972). Evolution and measurement of species diversity. *Taxon*, 21(2/3), 213–251.