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REVIEW

Optimising sampling methods for small mammal communities in Neotropical rainforests

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ABSTRACT

1. Quantifying mammalian biodiversity is a critical yet daunting challenge, particularly in species-rich ecosystems. Non-volant small mammals account for >60% of the mammalian diversity and often require several survey methods to estimate their species richness and abundance, because of differences in their size and behaviour.
2. Using 117 studies at 278 sites in a species-rich biome, the Brazilian Atlantic Forest, we determined the influence of trap configuration, trap type, and sampling effort on measures of species richness and abundance.
3. We used generalised linear mixed-effects models to determine which methodological approaches influenced estimates of species richness and abundance at the sampling sites. We used estimates of beta (β) to determine which methods improved species richness and abundance estimates, and generated predicted values for the overall species richness as a function of trap configuration (line transect, grid, or both), trap type (pitfall traps, live-traps or both), and sampling effort (number of trap-nights).
4. Our results indicated that sites in which pitfall traps alone were used generated higher estimates of the overall small mammal species richness and abundance, and rodent abundance, than sites in which only live-traps were used. Sites in which pitfall traps alone were used also produced higher estimates of species richness and abundance, and rodent species richness and abundance, than sites in which both trap types were used. Increased sampling effort led to increased estimates of species richness, but sites in which pitfall traps were used alone or together with live-traps had higher estimates of species richness with less sampling effort than sites in which live-traps only were used. Using pitfall traps greatly reduced the number of trap-nights necessary to obtain a good estimate of small mammal species richness in a community.
5. We found no influence of trap configuration (line transects or grids) on estimates of species richness, but the abundance of rodents was estimated to be higher in sites where both line transects and grids were used, than in sites where only one trap configuration was used.
6. Our review shows the importance of using pitfall traps in research, monitoring, and environmental impact studies on species-rich small mammal communities.

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INTRODUCTION

Biodiversity, commonly measured as the number of species in a system (i.e. species richness), is a major determinant of community dynamics and ecosystem function (Tilman et al. 2014). Ecologists have tried to find efficient and effective ways to quantify species richness, but communities are often populated by species that respond to sampling effort differently because of variations in their life histories, movements, sizes, and functional characteristics (Simberloff 1986, May 1988, Gaston 2000, Purvis & Hector 2000, Karp et al. 2012). How well ecologists are able to quantify a diverse community of species is influenced by the sampling design and methods they use (Gotelli & Colwell 2001, Ribeiro-Júnior et al. 2011, Cardoso et al. 2014). Thus, determining which designs and methods are best for quantifying species richness and abundance in small mammal communities is critical to advancing our understanding of their ecology and conservation.

Non-volant small mammals (<1 kg), mostly belonging to Afrosoricida, Didelphimorphia, Erinaceomorpha, Rodentia, and Soricomorpha, represent more than 60% of all species of mammals (Wilson & Reeder 2005). They occupy a variety of ecological niches (Wilson & Reeder 2005), and they have been associated with ecological functioning, environmental health and zoonotic diseases (Davis et al. 2005, Hill & Brown 2011, Halliday et al. 2012, Oliveira et al. 2013). Small mammals play key roles in an ecosystem, serving as seed dispersers, predators (Pizo 1997, Brewer & Rejmanek 1999, Vieira & Izar 1999, Vieira et al. 2003, Galetti et al. 2015), and mycorrhizal fungus dispersers (Janos & Sahley 1995, Johnson 1996). Small mammal communities have also been used to support conservation decisions (Banks-Leite et al. 2014, Dambros et al. 2015) and to measure environmental quality (Pickett et al. 2001, Pardini et al. 2010, Lira et al. 2012, Costa et al. 2014, Caudill et al. 2015).

To understand small mammal communities and their emergent properties, ecologists have developed various methods to estimate their diversity and composition (Fleming 1975, O'Farrell et al. 1994, Voss et al. 2001, Hice & Schmidly 2002). Numerous methods are used to capture small mammals (Jones et al. 1996, Reis et al. 2014), but little is known about how to maximise estimates of species richness in diverse communities (Thompson et al. 2007). The need to establish effective small mammal sampling protocols is especially relevant where species richness is high and knowledge is limited. It is in these speciose regions that measures of biodiversity are commonly used to determine where conservation resources should be directed (Banks-Leite et al. 2014, Marchese 2015).

A number of factors, such as seasonality (Vieira et al. 2014), moon phases (Maestri & Marinho 2014), and bait type (Astúa et al. 2006), which can influence the probability of small mammal captures, are a challenge for researchers to control. Therefore, it is necessary to have higher control of other factors that influence small mammal capture probabilities. Researchers must decide on the trap configuration (how to place traps), what type of traps to use, and how much sampling effort to use.

Researchers often choose between two trap configurations: either linear transects or rectangular grids (Pearson & Ruggiero 2003). Many trap types are used to capture small mammals (Woodman et al. 1996, Voss et al. 2001, Santos-Filho et al. 2006, Belant & Windels 2007), but live-traps were widely

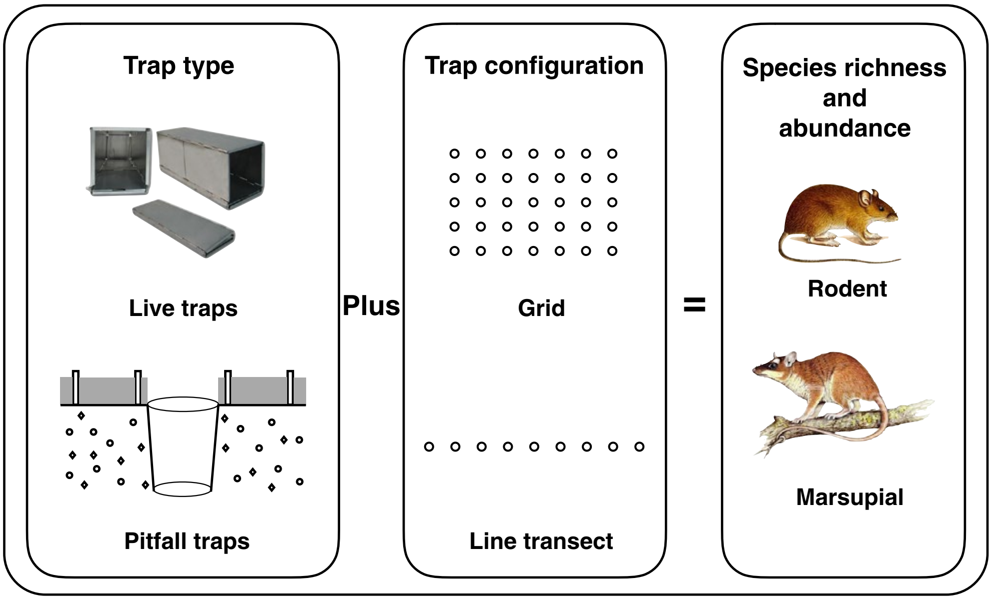

Fig. 1. We assessed how methods used affected estimates of small mammal species richness and abundance in tropical forests. We also considered the sampling effort (number of trap-nights). [Colour figure can be viewed at wileyonlinelibrary.com]

accepted as the best for sampling small mammals (Slade et al. 1993, O'Farrell et al. 1994, Santos-Filho et al. 2006). More recently, researchers have found that the use of pitfall traps may increase their ability to sample small mammal communities and individuals (Gotelli & Colwell 2001, Umetsu et al. 2006, Caceres et al. 2011, Ribeiro-Júnior et al. 2011, Santos-Filho et al. 2015). Researchers also need to determine how much sampling effort to employ, and there has been enormous variation in the sampling effort used to estimate species richness and abundance (Steele et al. 1984, Thompson et al. 2007).

To investigate how researchers' decisions affect the outcomes of studies of small mammals, we analysed a dataset of 117 studies conducted in 278 sites in the Atlantic Forest of South America. This is the largest and most comprehensive dataset on small mammal communities in a tropical region. We evaluate how trap configuration, trap type and sampling effort affect estimations of species richness and abundance of marsupials and rodents (Fig. 1).

METHODS

Study area

The Atlantic Forest was one of the largest rainforests in the Americas, originally covering around 150 million hectares along the Brazilian coast and extending into parts of Argentina and Paraguay (Galindo-Leal & Câmara 2003, Ribeiro et al. 2009; Fig. 2). Currently, fragmented patches

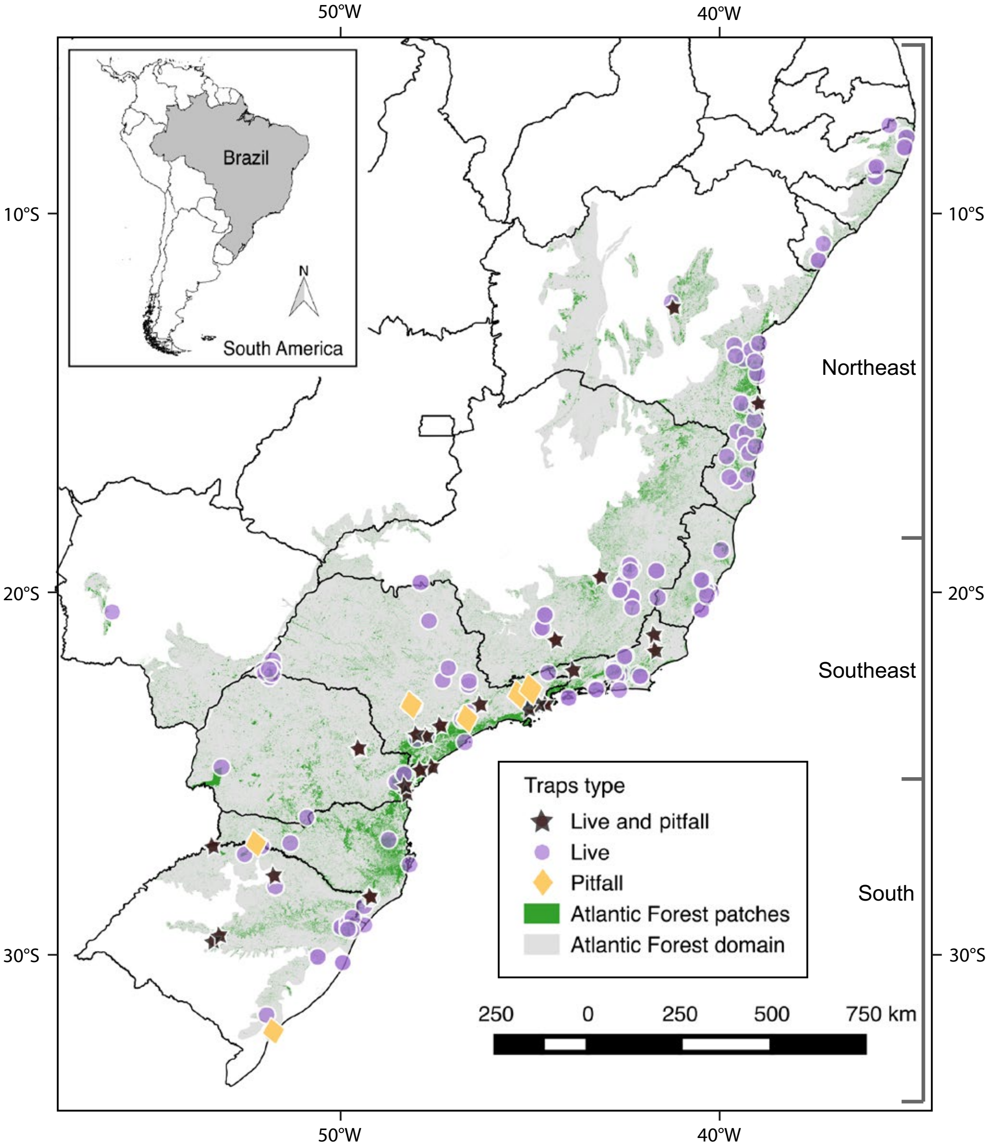

Fig. 2. Locations of the 278 sites in the Brazilian Atlantic Forest where studies on small mammal communities were conducted using pitfall traps (diamonds), live-traps (circles) and live-traps and pitfall traps together (stars). [Colour figure can be viewed at wileyonlinelibrary.com]

of Atlantic Forest cover <12% of its original area, and most of the fragments are small and highly defaunated (Ribeiro et al. 2009, Jorge et al. 2013). The Atlantic Forest hosts 22 species of marsupial (Didelphidae) and 97 species of small rodent (Caviidae, Cricetidae, Ctenomyidae, Echimyidae, Muridae, and Sciuridae; Paglia et al. 2012).

Small mammal assemblage database

We conducted a literature review of English and Portuguese studies of small mammals in the Atlantic Forest using the search tools Google Scholar and Web of Science with the following key words: small mammal(s), survey(s), inventory (inventories) and Atlantic Forest. We also performed searches in the unpublished literature, such as dissertations and scientific reports. For our analysis, we included only studies in which individual mammals were captured on the ground or less than 1.5 m above the ground, in rectangular sheet-metal cage live-traps (e.g. Sherman, H.B. Sherman Traps, Inc., Tallahassee, Florida, USA), rectangular wire metal cage live-traps (e.g. Tomahawk Inc., Hazelhurst, Wisconsin, USA), or pitfall traps (buckets dug into the ground, with drift fences), and in which appropriate geographical references for the forest remnants sampled were provided. From the sites included in these studies we compiled a dataset including site location, region (south, southeast and northeast Brazil), patch size (size of the forest fragment), trap configuration (line transect, grid, or both), trap type (pitfall traps, live-traps, or both), and sampling effort (total trap-nights). For each site, we noted the presence or absence of all small mammal species found in the Atlantic Rainforest.

The distance between traps or traps/ha (density of traps) can be used a measure of sampling effort (Pearson & Ruggiero 2003), but most studies did not report this information, and the density of traps could only be estimated for trapping grids (used in 27% of sites), so we used the number of trap-nights to estimate sampling effort by trap type (pitfall traps or live-traps). We did not have enough information to discriminate between traps based on build, size, design, hooks, or trigger sensitivity. It is well-known that the configuration of traps (line transect or grid) should depend on the purpose of the study (Pearson & Ruggiero 2003), but we considered the influence of survey methods specifically on the estimates of species richness and abundance of small mammals (Pearson & Ruggiero 2003).

Data analysis

We used generalised linear mixed-effects models (glmer) in the package lme4 (Bates et al. 2014) for the R platform (Anonymous 2016) to determine which methodological approaches resulted in greater measurers of species richness and abundance of small mammals. For each site, we calculated species richness as the overall number of species of rodents, marsupials and both groups combined. We estimated the sampling effort used in each site by multiplying the number of traps used with the number of sampling nights. We estimated the abundance of small mammals from the overall trap success, a measure of catch per unit effort (total individuals captured/sampling effort).

We created six separate models to compare trapping methodologies based on the species richness and abundance of rodents, marsupials and both combined. All models included a continuous variable for sampling effort and categorical variables for survey methods (line transect, grid, or both) and trap type (live-traps, pitfall traps, or both). We fitted the models to either a Poisson or Gama distribution with a log link, based on the distribution of the data as determined by deviance (Simonoff 2013). We checked our variables for collinearity and removed variables with $r > 0.60$. Additionally, we included two random effects in each model (region and patch size) to account for the variation in species richness in different regions (south, southeast, and northeast; the greatest species richness was in the southeast [85 species], the lowest was in the northeast [34 species]) and in patch sizes ranging from 0.15 ha to 185300 ha. We know that species richness increases with patch size in the Atlantic Forest (Pardini et al. 2010). We considered variables for which estimates of beta (β) had 95% confidence intervals that did not include zero to be significant predictors of species richness or abundance. To facilitate multiple pairwise comparisons of categorical variables we used the general linear hypothesis test (glht) in the multcomp package for R, which adjusts for multiple comparisons (Hothorn et al. 2008). To help us interpret our results we generated predicted values for species richness based on the sampling effort and type of traps used, by using the predictSE function in the AICcmodavg package for R (Mazerolle 2016).

RESULTS

In total, after discarding four studies in which information was duplicated and four from which information about survey methods was missing, we found 117 references, 56 in Portuguese and 61 in English. Our references included one unpublished dataset, one conference report, one book chapter, 35 theses and 79 peer-reviewed papers, documenting studies of small mammal communities at 278 sites in the Atlantic Forest of Brazil (Appendix S1). We considered our sample size to be the number of sites. We failed to find studies on small mammals in the Atlantic Forest of Paraguay and Argentina. At least one paper was published 30 years before we conducted our review, but 80% were published after 2000.

The communities were located in different biogeographical regions of the Atlantic Forest: 41 small mammal trapping sites were located in the northeast, 178 in the southeast and 59 in the south (Fig. 2). The mean of forest patches studied were 8187 ha (0.15–185300; n = 278). The mean total sampling effort was 6639 trap-nights (27–94318; n = 278), for live-traps it was 6475 trap-nights (27–94318; n = 207), for pitfall traps it was 3651 trap-nights (893–6500; n = 13), and for both trap types it was 7894 trap-nights (88–50416; n = 58; Appendix S2). There was no significant variation in the sampling effort (trap-nights) that could be attributed to trap types (pitfall trap, live-traps and both; ANOVA; F = 0.83, P = 0.43). The seasonality of sampling effort varied: at 11 sites, trapping took place only in the dry season, at 7 only in the wet season, at 237 in both seasons, and in 23 sites, researchers did not report the seasonality of trapping. We conducted a post-hoc analysis (generalised linear model) on our data to determine whether the trapping season influenced species richness, and found no evidence that season was a relevant predictor of species richness (the 95% confidence intervals of all βs included zero, so were not significant).

Our dataset included 105 species of small mammal from two Orders: Didephimorphia (13 genera, 26 species), and Rodentia (37 genera, 79 species; Appendix S3). Species richness mean was 8.2 species (1–23) per site. At least one of the three exotic species (*Rattus rattus*, *Rattus norvegicus*, and *Mus musculus*) was present at 24% of the sites. At 74% of sites, only live-traps were used, at 5%, only pitfall traps were used, and at 21%, both trap types were used. At 72% of the sites, traps were configured on line transects, at 24%, traps were placed on grids, and on 4%, they were placed on both line transects and grids.

Sampling effort (trap-nights) was positively correlated with the estimated species richness of rodents (n = 265, β = 0.093, 0.043–0.143), marsupials (n = 253, β = 0.133, 0.077–0.188), and marsupials and rodents together (n = 278, β = 0.145, 0.074–0.215) but was not correlated with our measure of abundance (Table 1, Fig. 3) that was derived from the sampling effort.

Table 1. Results of model selection comparing trapping methodologies used to estimate species richness and abundance of rodents, marsupials and both combined at 278 sites. All models include a continuous variable for sampling effort, and categorical variables for trap configuration (line transect, grid or both), and trap type (live-traps, pitfall traps or both). Beta estimates (β), standard error (SE), confidence intervals (95% CI) and significant predictors of species richness and abundance (*) are shown.

	Species richness				Abundance			
	β	SE	95% CI	Sig.	β	SE	95% CI	Sig.
Marsupials								
Effort	0.133	0.028	0.077–0.188	*	−0.021	0.080	−0.178–0.136	
Trap type								
Live-trap	−0.223	0.087	−0.393 to −0.052	*	0.179	0.190	−0.194 to 0.552	
Pitfall	−0.180	0.176	−0.526 to 0.166		−0.325	0.376	−1.061–0.412	
Both	0.043	0.166	−0.282–0.367		−0.504	0.348	−1.185–0.178	
Trap configuration								
Grid	0.066	0.204	−0.334–0.466		0.226	0.439	−0.635–1.087	
Line transect	0.075	0.199	−0.315–0.465		0.288	0.427	−0.549–1.125	
Both	0.009	0.080	−0.148–0.167		0.062	0.172	−0.275–0.40	
Rodents								
Effort	0.093	0.025	0.043–0.143	*	−0.099	0.069	−0.235–0.036	
Trap type								
Live-trap	−0.291	0.068	−0.424 to −0.158	*	−0.194	0.163	−0.513–0.124	
Pitfall	0.358	0.117	0.129–0.588	*	0.952	0.323	0.32–1.584	*
Both	0.649	0.108	0.438–0.861	*	1.146	0.299	0.56–1.732	*
Trap configuration								
Grid	−0.205	0.156	−0.509–0.10		−0.851	0.379	−1.593 to −0.109	*
Line transect	−0.138	0.150	−0.432–0.156		−0.946	0.368	−1.668 to −0.223	*
Both	0.066	0.064	−0.059–0.192		−0.094	0.148	−0.385–0.196	
Marsupials and Rodents								
Effort	0.145	0.036	0.074–0.215	*	0.035	0.044	−0.051–0.121	
Trap type								
Live-trap	−0.233	0.080	−0.39 to −0.077	*	0.240	0.172	−0.097–0.577	
Pitfall	0.201	0.156	−0.104–0.506		0.864	0.350	0.178–1.550	*
Both	0.434	0.143	0.154–0.715	*	0.624	0.326	−0.016–1.263	
Trap configuration								
Grid	−0.105	0.177	−0.452–0.243		0.109	0.370	−0.616–0.834	
Line transect	0.000	0.172	−0.338–0.337		0.244	0.355	−0.452–0.940	
Both	0.104	0.072	−0.037–0.246		0.135	0.174	−0.206–0.476	

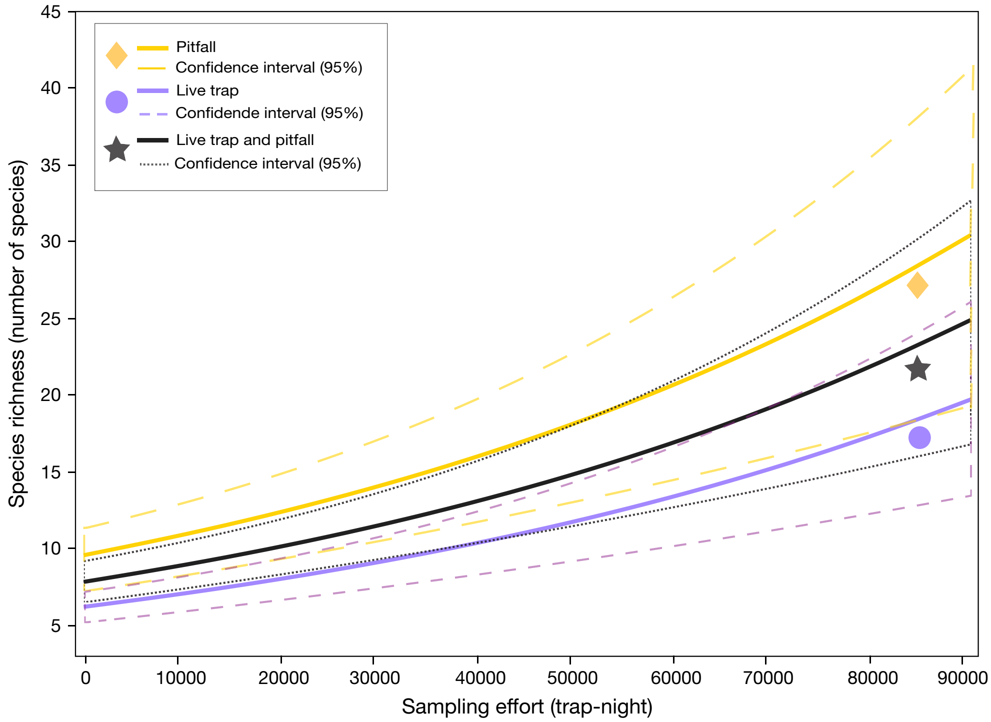

Fig. 3. Predicted values for species richness in relation to trap type and sampling effort (trap-nights): pitfall traps (diamonds) live-trap (circles) and live-trap and pitfall traps together (stars), with 95% confidence intervals (dashed lines). [Colour figure can be viewed at wileyonlinelibrary.com]

For marsupials, using only live-traps resulted in lower estimated species richness (β = −0.233, −0.393 to −0.052) than at sites where both pitfall traps and live-traps were used. For rodents, using pitfall traps alone resulted in higher estimates of species richness and abundance than at sites where live-traps alone were used (richness β = 0.649, 0.438–0.861; abundance β = 1.146, 0.299–0.560) and at sites where both methods were used (richness β = 0.358, 0.129–0.588; abundance β = 0.952, 0.32–1.584). Furthermore, at sites where live-traps were used, rodent species richness was estimated to be lower than that at sites where both pitfall traps and live-traps were used (β = −0.291, −0.424 to −0.158). For marsupials and rodents together, the use of pitfall traps alone resulted in higher estimates of species richness than the use of live-traps (β = 0.434, 0.154–0.715), and the use of live-traps resulted in lower estimates of species richness than the use of both trap types (β = −0.233, −0.390 to −0.077). There was no difference between the estimated species richness at sites in which pitfall traps alone and both trap types were used, for marsupials and rodents together (Table 1). Additionally, abundance was estimated to be higher at sites where only pitfall traps were used than at sites where live-traps or both trap types were used (β = 0.864, 0.178–1.550).

Trap configuration had no influence on estimated species richness and abundance for marsupials and rodents together. However, more rodents were caught at sites in which both transects and grids were used than at sites where just grids or transects were used (compared with lines β = −0.946, −1.668 to −0.223; compared with grids β = −0.851, −1.593 to −0.109; Table 1). The use of pitfall traps greatly reduced the number of trap-nights necessary to obtain good estimates of small mammal species richness in a community. The sampling effort needed to capture 90% of the species richness (14.6 species) using both live-traps and pitfall traps was reduced to 48500 trap-nights, compared with the 67000 trap-nights needed when using live-traps alone. Similarly, the sampling effort needed to capture 75% of species richness (11 species) was reduced from 40000 to 22900 trap-nights (Fig. 3).

DISCUSSION

In reviewing sampling methods for small mammals in Neotropical forests, we found that the use of pitfall traps led to greatly increased estimates of species richness and abundance. We suggest that pitfall traps should be used in future studies involving monitoring and surveying small mammals in Neotropical forests. To the best of our knowledge, this is the first review of extensive data on trapping methodologies that has been conducted for small mammals; it reinforces the need to investigate the best methods for estimating biodiversity in species-rich groups.

The use of pitfall traps has been recognised as an important capture technique to improve species richness and abundance estimates of small mammals for two main reasons. First, pitfall traps do not depend on the attraction of animals to a bait (Sealander & James 1958, Williams & Braun 1983, Astúa et al. 2006); they capture all animals that try to pass over each trap, and are especially effective if drift fences are used (Bury & Corn 1987, Ellis & Bedward 2014, Stromgren & Sullivan 2014). Second, the capture of one individual in a pitfall trap does not prevent the capture of other individuals, as is the case for live-traps, that may frequently be occupied by abundant and common species (Umetsu et al. 2006). However, many researchers avoid using pitfall traps because their use requires the labour-intensive burying of buckets and installation of fences on the ground. Also, pitfall traps may be perceived as kill traps, but there are a number of options that can greatly limit the number of accidental deaths (Barros et al. 2015). To reduce the probability of accidental death, pitfall traps need daily maintenance to remove water, any captured animals and bycatch (Barros et al. 2015).

Studies on small mammals in which pitfall traps are not used are likely to provide underestimations of species richness. A previous study in the Atlantic Forest showed that large pitfall traps captured more than twice the number of individuals (abundance) and approximately three times the number of species (richness) per study site than live-traps, including several rare species not captured in live-traps (Umetsu et al. 2006, Barros et al. 2015). Nonetheless, obtaining higher proportions of rare species does require more sampling effort. Pitfall traps also appear to have higher total capture success than live-traps placed on or near the ground (Vieira et al. 2014). Similarly, studies have shown that pitfall traps were three to eight times more efficient for capturing young individuals than live-traps, depending on habitat type (Lyra-Jorge & Pivello 2001, Hice & Schmidly 2002, Umetsu et al. 2006). Some authors also suggest that live-traps do not capture young individuals or light species because of the trigger sensitivity (Maddock 1992, Lyra-Jorge & Pivello 2001, Francl et al. 2002, Barros et al. 2015). In addition, Barros et al. (2015) showed that live-traps of different sizes are more efficient, or less efficient, for specific groups of small mammals. Indeed, the use of live-traps with different designs or trigger systems may explain variation in local capture success (Nicolas & Colyn 2006, Santos-Filho et al. 2006, Umetsu et al. 2006). We focused on broad differences in trap efficacy, regardless of trap size. We have no evidence that considering trap design or trigger sensitivity of live-traps would have modified our main conclusion, that the use of pitfall traps improves estimates of species richness and abundance.

A few researchers found live-traps to be more efficient than pitfall traps (Petersen 1980, Laurance 1992, Santos-Filho et al. 2006, Dizney et al. 2008); however, in these studies, shallow pitfall traps (in general <40 cm depth) were used, which may have allowed more animals to escape (Thompson et al. 2005). Additionally, research has shown that the configuration of live-traps in the understory and canopy layer may influence capture success, but not necessarily estimates of species richness (Taylor & Lowman 1996, Graipel et al. 2003, Astúa & Geise 2006). Higher capture success using live-traps has also been found for studies targeting a single species (Boonstra & Rodd 1984) or conducted in specific geographical regions (Friend et al. 1989, Torre et al. 2010).

Some researchers have suggested that the arrangement of traps for sampling small mammals influences estimates of community composition (Pearson & Ruggiero 2003, Ribeiro-Júnior et al. 2011), and contrasting conclusions have been reached regarding the best arrangement of traps for estimating species richness. Some researchers suggest that line transects are better than grids (Pearson & Ruggiero 2003), whilst others have found grids to be better than line transects (Bujalska 1989). We did not find any influence of the configuration of traps (line transects, grids, or both) on species richness. We found that using both grids and line transects together at the same site resulted in increased estimations of the abundance of rodents. Combining these two trap configurations may be the best approach when the goal is to maximise rodent captures. Indeed, grids and line transects are both widely used to quantify the abundance of small mammals (D'Andrea et al. 1999, Pardini et al. 2005, Pacheco et al. 2013). Nonetheless, grid-based studies may have some advantages, including providing the ability to estimate the movements easily (e.g. ranges, maximum distances) and to collect data on population dynamics (e.g. survival, fecundity, abundance; (Pelikan et al. 1964, Puttker et al. 2013). Nevertheless, the distance between traps in grids or line transects (i.e. the density of traps) may influence estimates of species abundance (Pearson & Ruggiero 2003), especially when rodents are being sampled (Pelikan et al. 1964, Barros et al. 2015).

Estimating species richness is an important goal for ecologists and conservationists. Numerous statistical tools are available to establish relationships between sampling effort and species captured (Colwell & Coddington 1994). Our study shows that sampling with pitfall traps optimises species captures over time, allowing ecologists to reach their goals faster than by sampling with live-traps alone. In most environmental impact studies, pitfall traps are not used; this may bias our understanding of the real diversity of small mammals. We believe that the use of pitfall traps should be legally required in the environmental impact studies involving the assessment of small mammal populations. We could not test for the effects of the use of arboreal traps in our analyses, because we found very few studies in which they were used (Grelle 2003, Vieira & Monteiro 2003, Hannibal & Caceres 2010), but their use may also increase our ability to sample arboreal rodents (e.g. *Echymis*, *Phyllomys*) and marsupials (*Caluromys*; Malcolm 1991).

In conclusion, our review indicates that small mammal trapping with live-traps alone results in a portion of rodent and marsupial species richness being missed, and that trapping with pitfall traps is required if one is interested in obtaining a comprehensive sample of small mammal communities. Though we were unable to evaluate the effects of using other types of traps, various baits, traps of different sizes and traps with various triggers, we stress that using both pitfall traps and live-traps together optimises the efficiency and effectiveness of sampling, and maximises the captures of small mammals in rodent and marsupial communities. Obtaining samples that capture a large portion of small mammal species richness in highly diverse ecosystems may only be possible with considerable sampling effort. Nevertheless, such sampling effort is necessary for informing conservation, environmental impact assessments, and landscape management, and to prioritise areas for conservation.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. The 117 publications on small mammal communities in the Atlantic Forest of Brazil.
Appendix S2. Scatter plot of $\log_{10}$ (sampling effort, in trap-nights) by species richness.
Appendix S3. List of small mammal species reported in the 117 references used in our study.

