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Forest conversion to cattle ranching differentially affects taxonomic and functional groups of Neotropical bats

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ABSTRACT

Understanding the effects of land conversion for livestock grazing on species diversity and functional groups continues to be urgently needed to assess how ranching affects animal assemblages and provide guidelines for managing landscapes under this omnipresent type of land use. Given Neotropical bats' high diversity of feeding habits and flying abilities, and that they play multiple, important ecological roles in ecosystems, they are an ideal study system to address such a need. We investigated the effects of livestock ranching on Neotropical bat species and functional groups composition via meta-analyses of published information. We used the odds-ratio metric to compare the frequency of occurrence of bat species in old-growth forest vs. areas influenced by livestock. Our results show no effects when considering bats as a group. However, significant effects emerge when they are assessed separately, on the basis of taxonomic family, feeding habit, conservation status and flying ability, showing that considering bats as a black box mutes relevant patterns. Molossid and phyllostomid species with high movement ability or omnivorous habit showed an increased frequency in livestock areas. In contrast, frugivores and aerial insectivores with low movement ability, carnivores, gleaning insectivores, nectarivores, sanguivores and species considered under some degree of extinction risk were significantly more frequent in old-growth forest. Overall, our results support that areas converted for livestock production retain only a subset of the Neotropical bat functional diversity while most of the functional groups are negatively impacted. Such heterogeneity of responses seems critical for our understanding of the effects of land use change on animal communities.

1. Introduction

With the burgeoning human population, anthropogenic disturbances impose increasing threats to biodiversity and ecosystem functioning, including major consequences on animal communities (Dirzo et al., 2014). Livestock grazing and cattle ranching have been recognized as one of the oldest and most geographically expansive forms of land use change (Diaz et al., 2007; Pielke et al., 2011). Livestock production has a number of negative environmental effects. The massive conversion of natural habitats into pastures has local, regional and global consequences in terms of greenhouse emissions, soil erosion, local and regional climatic regulation, biodiversity loss, and can compromise ecosystem services like pollination, control of pests, flood and water, all of them aspects of considerable concern, particularly in the case of tropical forests (Nicholson et al., 1995; Laurance et al., 2014; Malhi et al., 2014; Laurance and Usech, 2009; Markl et al., 2012; Galetti and Dirzo, 2013; Corlett, 2013). In those converted areas, due to trampling and constant passage of cattle across the landscape, cattle ranching leads to increased soil exposure and decreased coverage of native herbaceous and shrub layers (Galindo-González and Sosa, 2003; Trolle, 2003), as well as considerable reductions of plant and animal species diversity (Galindo-González and Sosa, 2003; Trolle, 2003; Diaz et al., 2007; Bobrowiec and Gribel, 2010). In contrast, the effects of cattle ranching on functional groups are still poorly studied. Therefore, understanding the effects of livestock grazing on key functional groups is urgently needed to address anthropogenic effects on ecosystem functioning and provide guidelines for managing ecosystems under current and future accelerated human impacts (Lindsey et al., 2013).

Neotropical bat assemblages are critical for biodiversity conservation and ecosystem functioning due to their high diversity of ecological roles in communities (Medellín et al., 2000; Castro-Luna et al., 2007; Meyer et al., 2010). While a readily expected response is increased abundance of vampire bats, such as *Desmodus rotundus*, which can feed largely on cattle (Greenhall et al., 1983; Greenhall and Schmidt, 1988), conversion of tropical forests into pastures may negatively affect bat species whose feeding habits are greatly associated to old-growth forest.

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In addition to grasses, pioneer trees and some shrubs dominate livestock-influenced areas (Bobrowiec and Gribel, 2010). Because pioneer plants frequently include fruit and nectar sources used by bats then some fruit- and nectar-feeding species that forage on disturbance-associated plants can increase (Cosson et al., 1999; Medellín et al., 2000; Castro-Arellano et al., 2009; Estrada-Villegas et al., 2010). Insectivorous bat species that are able to roost in human-made structures in the ranches could be expected to increase as well (Bernard and Fenton, 2003). Such a response would be expected from bats that exhibit broad dispersal abilities and behavioral plasticity in response to those changes in resource availability (Fischer, 1992; Medellín and Equihua, 1998; Medellín et al., 2000; Meyer and Kalko, 2008; Farneda et al., 2015). In addition to food availability, persistence in degraded habitats may depend on their mobility and wing morphology (Meyer et al., 2008). For example, it is known that a higher aspect ratio (long and narrow wings) and relative wing loading of bats indicate higher flexibility in the use of space and ability to move among areas, influencing, in turn, how they use the existing resources (Farneda et al., 2015).

These documented patterns, however, emerge from a number of isolated examples, but no comprehensive, systematic evaluation assessing the consistency of patterns has been conducted. To address this lacuna, in this study we investigated the effects of land use change for livestock production on Neotropical bats using a series of meta-analyses (see Gurevitch and Hedges, 1999), based on the available literature, to examine two questions. First, to what extent do livestock areas affect Neotropical bat assemblages, and does the magnitude and direction (positive or negative) of effects depend on functional groups and flying abilities of the bat species? Second, to what extent phylogenetic identity and conservation status determine bat responses to livestock disturbance? Our analysis shows that multiple functional groups and most bat families, with the exception of some phyllostomids and molossids, are negatively impacted by forest conversion to cattle grazing, and suggest that this prevalent form of land use can compromise several ecological functions provided by the Neotropical bat community.

2. Materials and methods

To identify responses of Neotropical bat assemblages to forest conversion to cattle grazing, we used the odds-ratio metric (Rosenberg et al., 2000) to compare the frequency of occurrence of bat species between native old-growth forest and areas influenced by livestock. We compiled data from studies published between 1990 and 2016 obtained from The Web of Knowledge (Thomson Reuters), Scientific Electronic Library Online-SciELO (BIREME-OPS-OMS), Google Scholar (GOOGLE) and the Journal Storage Project-JSTOR (ITHAKA). We conducted extensive searches with combinations of the following keywords: *bat community*, *bat diversity change*, *bat assemblage*, *habitat modification*, *land use change*, *habitat loss, cattle ranching* and *livestock*. Searches on titles and abstracts of publications returned over 200 publications. We then selected studies in the Neotropics that compared bat assemblages between preserved forests and at least one local, adjacent site subjected to cattle ranching for livestock. We included only studies in which mist nets were used to sample bats to standardize the results of the meta-analyses and to avoid biases that might be introduced by different sampling methods. This filtering returned nineteen studies (Fig. 1), including 12 peer-reviewed articles published between 1992 and 2015, four theses and three technical reports that met our criteria (see Supporting information – Appendix A1). Considering each bat species recorded in each locality as a “study case”, the meta-analysis had 1024 study cases that covered the occurrence of 104 bat species in nine Latin American countries (see Supporting information).

For the analyses, we classified species reported in the selected articles according to their families, namely: Emballonuridae, Molossidae, Mormoopidae, Natalidae, Noctilionidae, Phyllostomidae and Vespertilionidae (following Simmons, 2005). For the analysis of responses depending on functional groups, we classified bats based on their main food items and the way in which they obtain such resources (feeding habit and abilities), into nine classes: nectarivore, sanguivore, carnivore, omnivore, gleaning insectivore, aerial insectivore with high wing loading and aspect ratio (wingspan^2/wing area), aerial insectivore with low wing loading and aspect ratio, frugivore with high dispersal abilities, and frugivore with low dispersal abilities (see Supporting information – Appendix A2 for a description of these traits and literature used). Finally, we also classified species according to their conservation status (IUCN, 2017): vulnerable, endangered or near threatened.

To classify the habitat types in which bats were recorded, we used the criteria provided by the authors of the original publications (see Supporting Information – Appendix A1). All of them refer to well-preserved sites, that is, old-growth forests with minimal anthropogenic or livestock disturbance. In livestock-influenced areas, degradation of the vegetation structure is evidenced by the absence of trees (or the presence of isolated forest patches or trees) and the fact that there is no understory due to trampling and constant passage of cattle over the vegetation and across the landscape. We compared the frequency of occurrence of bat species between old-growth forests and livestock-influenced areas.

We transformed the odds ratios to natural logarithms, as suggested by Rosenberg et al. (2000) and determined overall habitat preferences of bats through calculation of average odds ratios for all the study cases, regardless of type of habitat (livestock-influenced or old-growth) or species categories (family, feeding habit, conservation status and movement ability), and calculated the 95% confidence intervals for these averages. If the average odds ratio was positive and significantly > 0 (i.e., confidence interval did not overlap with zero), then bats were considered to be significantly associated with old-growth forests. When confidence intervals of average odds ratio included zero, species were then considered to show no preference for either type of condition. If the average odds ratio was negative and significantly < 0 (i.e., confidence interval did not overlap with zero), then bats were considered to be significantly associated with livestock-influenced areas. Analyses included only groups with more than five study cases to avoid biased results (Rosenberg et al., 2000). We run all analyses in R program with the metafor package (Viechtbauer, 2010)

3. Results

Phyllostomidae was the most represented family (76 species, 7353 individuals in 19 publications), followed by Vespertilionidae (14 species, 84 individuals in 13 publications), Molossidae (6 species, 29 individuals in 7 publications), Emballonuridae (3 species, 29 individuals in 6 publications), Mormoopidae (3 species, 296 individuals in 8 publications), Noctilionidae (1 species, 26 individuals in 4 publications) and Natalidae (1 species, 5 individuals in 3 publications) (Table 1 and Supporting Information).

The global effect size, including all species from all studies, indicated no difference of bat assemblages between old growth and livestock-influenced forests (Fig. 2). However, different patterns occurred when species were grouped into taxonomic, functional or conservation status classes. Bat species considered under some degree of extinction risk by IUCN (2017) – *Bauerus dubiaquercus*, *Vampyrum spectrum*, *Leptonycteris yerbabuenae* (near threatened), *L. curasoae*, *Musonycteris harrisoni*, *Balantiopteryx io* (vulnerable), and *Lonchophylla dekeyseri* (endangered) – were most frequently recorded in old-growth forests, whereas the least concern species were more frequently within livestock-influenced areas (Fig. 3a). Noctilionidae, Natalidae, Vespertilionidae, Emballonuridae and Mormoopidae bats were more frequently recorded in old-growth forests, while Molossidae presented no difference between old growth and livestock-influenced areas (Fig. 3b). On the other hand, Phyllostomidae was positively associated with live-

Fig. 1. Location of study sites and number of species and studies included in the meta-analysis of the effects of land use for cattle ranching on Neotropical bat assemblages.

stock-influenced areas (Fig. 3b). However, Phyllostomidae lost 13 bat species when land use changed from old-growth forest to livestock-influenced areas. Within this family, the subfamily Stenodermatinae lost six species, followed by Phyllostominae (5 species) and Glossophaginae (2 species). Vespertilionidae was the second most affected family (4 species), followed by Emballonuridae (1 species) (Table 1).

When bat occurrence frequency was analyzed on the basis of feeding habits and movement capacity, frugivores with high dispersal abilities (3986 individuals, 5 species), aerial insectivores with high wing loading and aspect ratio (29 individuals, 7 species) and omnivores (91 individuals, 2 species) were more frequently recorded in livestock-influenced areas than in old-growth forests (Fig. 3c). In contrast, the occurrence frequency of aerial insectivores with low wing loading and aspect ratio (440 individuals, 22 species), carnivores (19 individuals, 3 species), gleaning insectivores (82 individuals, 17 species), nectarivores (582 individuals, 12 species), sanguivores (341 individuals, 3 species) and frugivores with low dispersal abilities (2273 individuals, 34 species) were significantly more frequently recorded in old-growth forests than in livestock-influenced areas (Fig. 3c).

Table 1
Number of species (and individuals) of bats from different taxonomic groups mist-netted in old growth forests and livestock-influenced areas, and number of species loses or gains from old-growth forests to livestock areas.

Family Subfamily	Old-growth forests	Livestock-influenced areas	Bat species loss	Bat species gains
Phyllostomidae				
Stenodermatinae	33 (2436)	27 (2920)	6	0
Phyllostominae	22 (95)	17 (97)	5	0
Glossophaginae	12 (344)	10 (238)	2[a]	0
Carolliinae	6 (560)	6 (323)	0	0
Desmodontinae	3 (216)	3 (125)	0	0
Vespertilionidae	14 (61)	10 (23)	4	0
Emballonuridae	3 (23)	2 (6)	1[b]	0
Molossidae	6 (3)	6 (26)	0	0
Mormoopidae	3 (239)	3 (57)	0	0
Natalidae	1 (3)	1 (1)	0	0
Noctilionidae	1 (25)	1 (1)	0	0

[a] One endangered species.
[b] One vulnerable species.

4. Discussion

The results of our meta-analysis indicate that Neotropical bats, as a whole group, seem not to be sensitive to land use change resulting from livestock grasslands. However, this is a misleading conclusion, as different patterns emerge when the responses to conversion of land to livestock areas are assessed separately on the basis of phylogenetic affinity (family), feeding habit, movement ability, or conservation status. Our analyses revealed that livestock ranching favors species grouped as omnivores, high-dispersal frugivores or aerial insectivorous with high wing loading and aspect ratio. Bat species within these categories are in the least concern class regarding threatening, which is consistent with their success in disturbed, livestock-influenced areas. On the other hand, our results support that most Neotropical bat

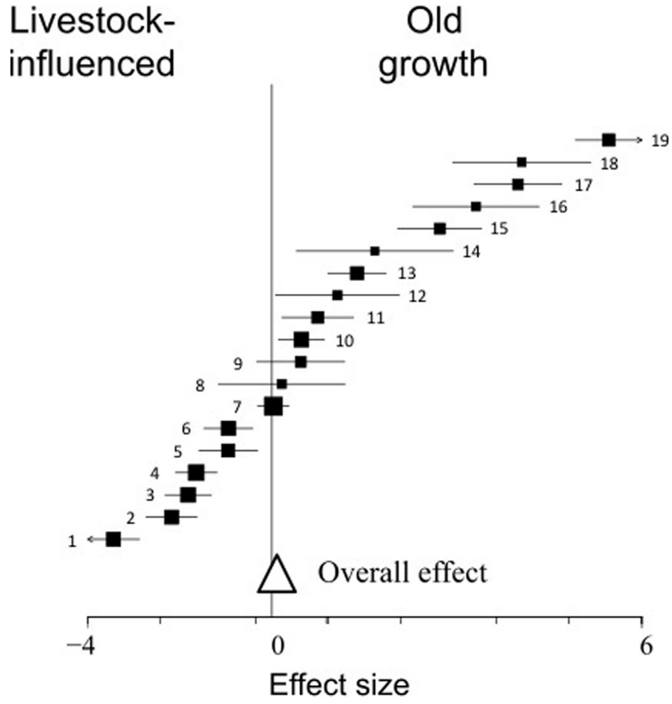

Fig. 2. Effect sizes (average odds ratios and 95% CI) between old growth and livestock-influenced areas estimated for bat assemblages of 19 compiled studies (cited as numbers; see references in Appendix A1). Effects are considered statistically significant when 95% CI does not overlap with zero. The size of the black squares is indicative of the number of "study cases", ranging from 7 (smallest square) to 31 (largest square).Effect sizes (average odds ratios and 95% CI) between old growth and livestock-influenced areas estimated for bat assemblages of 19 compiled studies (cited as numbers; see references in Appendix A1). Effects are considered statistically significant when 95% CI does not overlap with zero. The size of the black squares is indicative of the number of "study cases", ranging from 7 (smallest square) to 31 (largest square).

families and species grouped as carnivores, nectarivores, sanguivores, low-dispersal frugivores, gleaning insectivores or aerial insectivores with low wing loading and aspect ratio depend on old-growth forests. In general, therefore, old-growth forests harbor a higher phylogenetic and functional diversity of bats than livestock-influenced areas. The case of sanguivores is of special interest, given that increased abundance of sanguivores was initially expected in livestock-influenced areas based on their potential ability for feeding on cattle blood (Greenhall et al., 1983; Greenhall and Schmidt, 1988). Thus, other factors rather than food availability likely negatively affect sanguivores in these areas.

Abundance of bats in the family Phyllostomidae increased in livestock-influenced areas, although a higher diversity of phyllostomids has been found in old-growth forests (Fenton et al., 1992; Medellín et al., 2000; Estrada-Villegas et al., 2010). These findings support that a small proportion of Phyllostomidae species are highly tolerant to and may take advantages of human land alterations (Avila-Cabadilla et al., 2009). Among studies included in our analyses, the most frequent phyllostomids in livestock-influenced areas were the frugivores *Artibeus jamaicensis*, *A. planirostris*, *A. lituratus*, *Uroderma bilobatum*, *Platyrrhinus lineatus*, *Sturnira lilium* and *Carollia perspicillata*. In addition, further studies have demonstrated an increase in abundance of a few frugivorous species following other types of disturbance (e.g. Meyer and Kalko, 2008; Medellín et al., 2000; Farneda et al., 2015). The family Molossidae, which seems indifferent between old growth and livestock-influenced areas (present study), is typically composed of aerial insectivores that forage in open areas and above canopy in forested sites (Galindo-González and Sosa, 2003), and several species commonly establish large colonies in manmade structures (Estrada-Villegas et al., 2010; Jung and Kalko, 2010; Williams-Guillén and Perfecto, 2011). Thus, they could keep successful populations under land changes associated to cattle ranching. However, in contrast to phyllostomids and molossids, abundance of other five families – Mormoopidae, Vespertilionidae, Natalidae, Emballonuridae and Noctilionidae – was consistently reduced in livestock-influenced forests, supporting that land changes associated to cattle ranching markedly and negatively affect overall diversity of Neotropical bat families.

Animalivorous bats, including carnivores, sanguivores, gleaning insectivores and aerial insectivores with low wing loading and aspect ratio are more abundant in old growth compared with livestock-influenced areas. This response could be expected for these predators because old growth forests offer increased roost availability (Voss et al., 2016) and better sites for foraging for abundant prey than sites affected by anthropic activities (Gorrensen and Willig, 2004; Bader et al., 2015). Thus, these functional bat groups appear to be the best for assessing effects of anthropogenic changes on Neotropical forests. The greater abundance of nectarivores and low dispersal frugivores in old growth forests compared with livestock-influenced areas likely reflects the

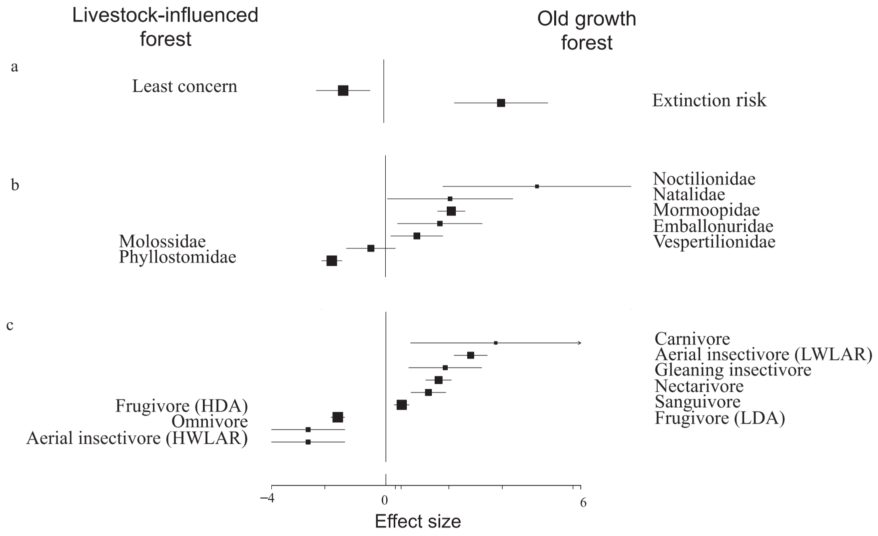

Fig. 3. Effect sizes (average odds ratios and 95% CI) between old growth and livestock-influenced forests estimated for bat assemblages depending on (a) conservation status by IUCN (2017), (b) bat families, (c) bat feeding habits and movement abilities. Effects are considered statistically significant when 95% CI does not include zero. The size of the black squares is indicative of the number of "study cases", ranging from 1 (smallest square) to 76 (largest square). Taxonomic group, traits and feeding guilds are noted, including HWLAR = aerial insectivores with high wing loading and aspect ratio; HDA = frugivores with high dispersal abilities; LWLAR = aerial insectivores with low wing loading and aspect ratio; LDA = frugivores with low dispersal abilities.

greater diversity of food sources and roosting places available in the former (Bernard and Fenton, 2003; Castro-Luna and Galindo-González, 2012). Livestock ranching appears to cause declines even for sanguivore bats, which could potentially feed on cattle blood (Greenhall and Schmidt, 1988). This seemingly unexpected result may stem from the fact that these bats can roost in tree cavities (Aguirre et al., 2003; Gomes and Uieda, 2004), the availability of which is reduced in livestock areas. Low availability of suitable shelter places in livestock areas would be an issue of relevance to *Desmodus rotundus*, which has often been recorded feeding on livestock (Greenhall et al., 1983). *Diphylla ecaudata* and *Diaemus youngi*, the other two species of sanguivore bats, have been suggested to feed mainly on bird blood (Greenhall et al., 1983; Carter et al., 2006). Therefore, another issue needing clarification is whether livestock can indeed represent profitable resource favoring these two species of sanguivores. Nonetheless, our results challenge the notion that land transformations for livestock ranching necessarily represent favorable conditions for the maintenance and proliferation of sanguivorous bats.

Livestock-influenced areas positively affected bat species with high movement ability or feeding flexibility. High wing loading and aspect ratio of aerial insectivores, typical attributes of molossids, confer high flight speed that make visits to isolated sites energetically cheap (Estrada-Villegas et al., 2010), and they appear to exclusively forage in unobstructed airspace outside or above forests (Norberg and Rayner, 1987; Clarke et al., 2005). Frugivores with high dispersal abilities are fast and energy-efficient flyers, while those with shorter and broader wings have higher maneuverability in cluttered habitats but incur in increased costs for commuting over longer distances (Norberg and Rayner, 1987; Estrada and Coates-Estrada, 2002; Henle et al., 2004; Ewers and Didham, 2006). Therefore, less dense understory and enhanced fragmentation in livestock-influenced areas can favor bats with low flying costs and broader diets, such as some frugivorous species with high dispersal ability (Medellín et al., 2000; Clarke et al., 2005; Willig et al., 2007; Meyer and Kalko, 2008; Meyer et al., 2008; Farneda et al., 2015).

Regarding bat conservation status, our results revealed old growth forest dependence among near threatened, vulnerable and endangered bat species, which supports habitat loss as a major driver of defaunation and species loss (Sala et al., 2000; Meyer and Kalko, 2008; Meyer et al., 2008; Dirzo et al., 2014; Farneda et al., 2015). Ongoing declines of bat populations are considerably less evident to humans yet arguably are functionally more important because they play pivotal roles on ecosystem services as dispersers, pollinators and predators (Kalka et al., 2008; Munin et al., 2012; Dirzo et al., 2014). The high-dispersal frugivores, represented by a few phyllostomid species positively affected by livestock-influenced areas, are seed dispersers of only a subset of the Neotropical bat-dispersed plants, frequently pioneer ones (Teixeira et al., 2009; Munin et al., 2012). Therefore, declines in pollination and seed dispersal of many old forest plants are expected in livestock-influenced forests, where nectarivores and low-dispersal frugivores are negatively affected. Likewise, livestock disturbance may compromise the control of prey populations and transport of nutrients across the landscape provided by animalivorous bats (Gonçalves et al., 2007; Kalka et al., 2008; Estrada-Villegas et al., 2010), as most of them showed dependence on old growth forests. Thus, different ecological functions are likely lost due to land change derived from livestock ranching. For instance, changes of pollinators or seed dispersers may drive selection of flower or fruit traits to match the increased availability of bats or other animals that effectively pollinate or disperse such plants (Mello et al., 2005; Thompson, 2005; Galetti et al., 2013).

Meta-analysis is particularly valuable for identifying large-scale patterns and facilitating evidence-based decision-making (Stewart, 2010; Harrison, 2011). Our results support that trait- and behavior-based approaches (e.g. movement ability), and feeding habits can provide more precise information on the effect of livestock land use. Overall, our results provide new discernments to guide landscape management, policy and practice to maintain or enhance bat populations and their ecological functions in ecosystems. A main highlight of this analysis is that (despite the high abundance of some phyllostomids and molossids observed in livestock-influenced forests) maintenance of old-growth forests is crucial for Neotropical bat ecosystem services conservation.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2017.04.021.

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