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Diel activity patterns of a canopy-inhibiting beetle community (Coleoptera) in a Neotropical rainforest

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Diel activity is one main feature of animal's behavior and is often an intrinsic trait characterizing distinct taxonomic groups. Abiotic conditions such as temperature may influence the diel activity patterns of arthropod communities associated with a particular ecosystem or habitat. Similarly, biotic factors, such as resource availability, affect arthropod activity. In addition, diel activity is thought to be an important factor in niche partitioning of arthropod communities. As part of a larger beetle survey in a lowland tropical rainforest in southern Venezuela, I analyzed the diel activity of an arboreal beetle community collected from 23 canopy-tree species over a cumulative year. Diel activity was observed in 535 beetle species, comprising 5,948 individuals, using a canopy crane installed in the study area. Of the 535 beetle species, 198 (37%) showed diurnal activity, and 281 (52.5%) showed nocturnal activity. In contrast, the proportions of nocturnal (n = 2,024, 34%) and diurnal (n = 1,983, 33.3%) individuals were balanced. Most of the observed beetles occurred only during the activity phase in their host trees. This particularly applies to extrafloral nectary- and flower-visiting beetle species. Flowering trees attracted different proportions of diurnal and nocturnal species according to flowering syndrome, whereas extrafloral nectaries were mainly visited at night. Thus, the beetle communities associated with single tree species showed distinct compositions of nocturnal and diurnal species.

KEYWORDS

diversity, Amazonas, canopy crane, community structure, Venezuela, plant-animal interactions

1 Introduction

Tropical rainforest canopies are in harsh environments. They receive high solar insolation during the day (Parker, 1995; Hallé, 1998), but exhibit high levels of water condensation at night (Blanc, 1990). As a result, the relative humidity and air temperature fluctuate significantly in the upper canopy (Pinker, 1980; Parker, 1995; Walsh, 1996; Szarzynski and Anhuf, 2001; Turton and Siegenthaler, 2004; Ulyshen, 2011). Nevertheless, adult insects are often more abundant and specious in the canopy than in the understory (Basset et al., 2001, 2015). Beetles associated with tree canopies are often highly diverse and abundant (Erwin, 1982; Stork, 1991; Basset and Arthington, 1992; Allison et al., 1993; Floren and Linsenmair, 1999). Like many other arthropods, most beetle species have a small

body size; therefore, they are strongly influenced by microclimatic conditions at the plant surface (Pincebourde and Woods, 2020; Pincebourde et al., 2021).

Beetles inhabiting this life zone are expected to develop specific strategies to overcome hygrothermal stress associated with rainforest canopies. One possibility is the use of different strata during the day and night; consequently, beetles may be present in the upper canopy only during their activity. Distinct patterns in the activities of arthropod communities are observed in different rainforest canopies. For instance, the canopy of a subtropical rainforest in Australia exhibits significantly higher activity of associated herbivores during the day (Basset and Springate, 1992). In contrast, Basset (1991) found high activity in an Australian subtropical rainforest tree species during the first part of the night. In Sulawesi, malaise trap samples revealed an extremely low level of night flight activity in major insect groups (Hammond, 1990). Basset et al. (2003) summarized more arthropod activity in the canopy during the day than at night. Generally, diel activity is correlated with habitat characteristics, such as temperature (Giménez-Gómez et al., 2018). The flight activity of dung beetles, for instance, is principally diurnal in the northernmost European regions (Koskela, 1979), whereas there are more crepuscular-nocturnal species in Mediterranean climates (Mena et al., 1989). In tropical and subtropical environments, the numbers of nocturnal and diurnal species are relatively similar (Cambefort, 1991; Gill, 1991). However, Feer and Pincebourde (2005) found that diurnal species were approximately twice as numerous and abundant as either nocturnal or crepuscular species in French Guiana, whereas other dung beetle communities showed dominance of nocturnal species in rainforests (Halffter and Matthews, 1966; Howden et al., 1991).

Organisms have evolved circadian clocks based on predictable 24-h environmental cycles (Paranjpe and Sharma, 2005; Rosbash, 2009; Brady et al., 2021). In insects, circadian clocks control the rhythmicity of several behaviors and physiological features, including locomotion and feeding (Saunders, 2002; Tomioka and Matsumoto, 2010; Franco et al., 2018). Thus, diel activity in insects is separated into hours of day and night (Fullard et al., 2000; Feer and Pincebourde, 2005). The diel activity of insects is often an intrinsic trait that causes uniform patterns in a single taxon (Kronfeld-Schor and Dayan, 2003; Boulter et al., 2005). Otherwise, diel activity may be adaptive and vary in accordance with the biotic conditions of the habitat. Diel activity can be affected by the quantity and quality of trophic resources (Martín-Piera et al., 1994). Brady et al. (2021) observed synchronization between the circadian clocks of Lepidoptera and their host plants. The variable caterpillar growth rate depends on diurnal feeding behavior in relation to the production of jasmonic acid in plants (Reymond et al., 2000; Jander et al., 2001; Kessler and Baldwin, 2002; Howe and Jander, 2008). Jasmonic acid triggers plant herbivore defense and shows peak accumulation in the middle of the day (Goodspeed et al., 2012).

Likewise, the diel activity patterns of communities may be the result of resource partitioning and facilitate coexistence (Hanski and Cambefort, 1991; Caveney et al., 1995; Palmer, 1995; Sowig, 1997; Krell-Westerwalbesloh et al., 2004). Niche partitioning has been discussed as one of the major reasons for high species diversity (Gause, 1934; Mayr, 1979). Consequently, temporal changes in community assemblages may be a common feature in many ecosystems, particularly in species-rich tropical rainforests.

For instance, the turnover between diurnal and nocturnal ant assemblages supports the coexistence of competitors (Albrecht and Gotelli, 2001; Hossaert-McKey et al., 2001; Luna et al., 2018).

In this study, I analyzed the diel activity of a canopy-inhabiting beetle community to clarify: (1) if the diel activity of canopy beetles is related to specific taxonomic groups indicating intrinsic traits; (2) if diel activity is linked to resource availability; and (3) if the diel activity of canopy beetles is linked to strata use.

2 Material and methods

2.1 Study area

The study site is located in the upper Orinoco region (Venezuela, state of Amazonas) and is part of the Man and Biosphere Reserve Alto Orinoco-Casiquiare. The region is a transitional zone between the Guyana-Highlands and the lowlands of the Río Negro-Casiquiare Basin (Winkler and Listabarth, 2003). The landscape is dominated by gently undulating peneplains interrupted by table mountains to the north. The Orinoco depression primarily contains Pliocene to recent alluvial deposits as well as denudation products of the Guyana-Highland (Gonzales et al., 1980; Gibbs and Barron, 1993). The soil structure and texture in the study plot are heterogeneous (Winkler and Listabarth, 2003) with ferralic arenosols and plinthichumic ferralsols (FAO-UNESCO, 1988), which prevail in the northern part.

The average annual precipitation in the study area is approximately 3,100 mm with year-to-year fluctuations of roughly 500 mm (Anhuf et al., 1999). A strong peak in annual precipitation occured from May to July, and a lower peak occurred in September and October. The canopy intercepted circa 18% of the annual precipitation in the study plot (Anhuf and Rollenbeck, 2001; Szarzynski and Anhuf, 2001) with large variations between the rainy and dry seasons, attaining values of 5% and 56%, respectively. The average annual temperature in the study area was approximately 26°C. Maximum temperatures during the day may reach 30.5°C and drop to only 20–21°C during the night. While the canopy receives the most solar radiation during the daytime, heat is lost through radiation and sensible and latent heat via condensation during the night. Accordingly, the temperature fluctuates by nearly 10°C in the upper canopy and only slightly near the ground (Anhuf and Rollenbeck, 2001; Szarzynski and Anhuf, 2001).

To access the tree tops, a large tower crane was installed in the study area close to the black water river Surumoni (3°10′N, 65°40′W; 105 m asl), a tributary of the Orinoco River. The canopy-crane system, 42 m in height, ran on a 120 m rail track. It covered an area of about 1.4 ha with its 40 m long swing. Using remote control, scientists could reach trees up to a maximum height of 35 m in a gondola. The crane was operated between 1995 and 2000.

2.2 Vegetation

The Surumoni area belongs to the Japura/Negro moist forest ecoregion (Dinerstein et al., 1995) or Imerí province (Morrone, 2014) which extends from Brazil to southern Venezuela, Colombia, and Peru. The study region is covered by a mosaic of lowland

rainforests, swamp forests, and savannas (Winkler and Listabarth, 2003). The vegetation of the crane plot is that of a moist lowland tropical rainforest classified as terra firme (Prance, 1979). The upper canopy usually ranges from 25 to 27 m in height, including a few emergent trees up to 35 m.

Altogether, 322 species of higher plants were identified in the 1.4 ha crane plot belonging to 208 genera from 78 families (Wesenberg, 2004). The species richest Spermatophyta were Fabaceae (23 species), Orchidaceae (19 species), Araceae (16 species), Rubiaceae (15 species), Lauraceae (13 species), and 10 species of Annonaceae and Chrysobalanaceae. The stem density of the area was 546 living trees per hectare, with an estimated 92 species per hectare. In 1999, there were 781 living trees $\geq$ 10 cm in diameter at breast height (DBH) belonging to 141 tree species within the crane plot. Frequent species in the tree fraction with a DBH $\geq$ 10 cm were *Goupia glabra* Aubl. (Goupiaceae), *Oenocarpus bacaba* Mart. (Arecaceae), *Dialium guianense* (Aubl.) Sandwith (Fabaceae), *Ocotea* aff. *amazonica* (Meisn.) Mez (Lauraceae), or *Ruizterania trichanthera* (Spruce ex Warm.) Marc.-Berti (Vochysiaceae) (Wesenberg, 2004). The most abundant species in the upper layer were *G. glabra, R. trichanthera,* and *D. guianense*. The abundant species in the middle layer were, for instance, *Couma utilis* (Mart.) Müll. Arg. (Apocynaceae), *O. bacaba*, and *Podocalyx loranthoides* Klotzsch (Picrodendraceae) (Wesenberg, 2004). Epiphytes and hemiepiphytes comprised 778 individuals from 53 species in 1996 (Engwald et al., 2000).

2.3 Beetle collection and observation

The sampling and observation of beetles comprised the following periods: September–November 1997, May–August and December 1998, and January–April 1999, thus enabling cumulative data collection for the aspect of a year. In addition, trap collection in October 1999 targeted a single tree species. License and authorization were issued under the number 15-1277 by Servicio Autonoma de Fauna, Ministerio del Ambiente y de los Recursos Naturales Renovables, Caracas, Venezuela.

Using the tower crane, crowns of tree species in the upper (approximately 25–30 m height) and middle canopy (approximately 18–25 m height) were searched regularly for Coleoptera during the day and night. A spotlight was used to enable nighttime observations. The plant parts sampled included leaves, small twigs, flowers, and fruits. The inventory of this canopy-beetle assemblage included 23 canopy-tree species (45 trees, 23 genera, 13 plant families). The observed beetles were captured by net, hand, branch, and foliage beating. However, these methods do not yield quantitative data. Additionally, aerial traps were used to collect flying beetles (Basset et al., 1997). These window traps consisted of two clear acrylic panels fixed over a cross, each with a length of 30 cm and height of 25 cm. A plastic tube, ending in a container, was placed beneath the panels. The container was filled with water mixed with surface-tension-diminishing detergent. The beetles were removed every two days. These traps provided semi-quantitative sampling results. A detailed description of the methodology and the trees selected for the survey was published in Kirmse (in prep.).

The collected beetles were stored in 70% ethanol. The beetles were assigned to morphospecies (hereafter species) and later, in part, identified by specialists. A complete list of all experts has been published in Kirmse (in prep.). Named genera in this study were determined by Alistair S. Ramsdale (Lycidae), Ubirajara R. Martins (Cerambycidae), Wills Flowers (eumolpine Chrysomelidae), Sergio Antonio Vanin (Curculionidae), and Brett C. Ratcliffe (Scarabaeidae). Carabidae, Dermestidae, and Meloidae were identified using Reichardt (1977), Pinto and Bologna (1999), and Háva (2004). Family group names follow Bouchard et al. (2011). Voucher specimens of the collected beetles were deposited at the Museo del Instituto de Zoología Agrícola "Francisco Fernandez Yepez," Maracay, Venezuela.

2.4 Diel activity of beetles

The beetle species were ecologically characterized according to canopy data and observations. Adult beetles and species were considered, regardless of the number of individuals observed and collected. The diel activity of the species was distinguished as either nocturnal or diurnal if all observed beetles showed the same activity. Species comprising individuals that were active during the day and night were categorized as "indifferent." Species with unknown activity (e.g., caught only in traps) were classified as "unknown." Activity includes all behaviors except passive (quiescent) resting, for example, locomotion including walking and flying, feeding, mating, or cleaning.

To characterize the entire community, I generalized the diel activity in a second step for single taxa as diurnal or nocturnal if all members ($n \geq 2$ spp.) were found to be active during either the day or night. This applies to two families (Buprestidae, Elateridae) and 11 genera (Carabidae: *Agra* Fabricius; Cerambycidae: *Acanthoderes* Audinet-Serville, *Agaone* Pascoe, *Chrysoprasis* Audinet-Serville; Chrysomelidae: *Entomochirus* Lefévre, *Nycterodina* Bechyné; Curculionidae: *Heilipus* Germar; Dermestidae: *Cryptorhopalum* Guérin-Meneville; Lycidae: *Idiopteron* Bourgeois, *Plateros* Bourgeois; Scarabaeidae: *Isonychus* Mannerheim).

Furthermore, the diel activity of all observed species was related to the diet used in the canopy. I distinguished general flower visitors, visitors to small white flowers with a generalized morphology, visitors to extrafloral nectaries, species utilizing extrafloral nectar and flowers, leaf feeders as well as other or mixed diets as diverse diets. The assignment of these "feeding guilds" was consistent with the plant parts sampled. A detailed description was published in Kirmse (in prep.).

The flowers were distinguished according to their commonly recognized flower syndromes (Faegri and Van der Pijl, 1979) to clarify possible specific associations between beetles and floral traits. Typical beetle flowers are open during the day and night and often award their visitors enormous quantities of pollen (Howe and Westley, 1986, 1988). Although the cantharophilous syndrome encompasses a broad range of floral structures (Irvine and Armstrong, 1990; Bernhardt, 2000), typical beetle flowers are commonly described as either flat or cup-shaped and of radial symmetry, allowing open access to their rewards (Howe and Westley, 1986; Frame, 2003). Their colors are often dull, white, or cream (Faegri and Van der Pijl, 1979; Howe and Westley, 1986; Willmer, 2011). I found seven tree species bearing this type of flower with a generalized morphology, whereas 13 tree species had dissimilar flowers.

I further analyzed the diel activity patterns of beetle communities associated with distinct phenological seasons of several tree species (flowering and leaf-flushing with active extrafloral nectaries) and beetle communities collected from distinct tree species for a cumulative year. I selected all of the most species-rich assemblages comprising most of the observed species. The inclusion criterion for the samples was at least 30 observed species comprising more than 40 individuals. To avoid bias caused by manual collection, I provided only data for trap samples for the most speciose communities. Other host-tree-related samples combined data from hand and trap collections.

Beetle communities visiting extrafloral nectaries were analyzed from two tree species of Chrysobalanaceae: *Licania hebantha* Mart. ex Hook. f. (one tree, two seasons) and *Moquilea subarachnophylla* (Cuatrec.) Sothers and Prance (five trees, one season) (Kirmse and Chaboo, 2019). These data combine trap and hand collection. The samples over a cumulative year included the following three tree species: *Goupia glabra* (two trees: trap sample), *Ruizterania trichanthera* (two trees: combined trap and hand collection), and *Senna* cf. *silvestris* (Vell.) H. S. Irwin and Barneby (Fabaceae) (one tree: combined trap and hand collection).

I separated flower-visiting beetle communities into two different groups according to flowering syndrome. The first group comprised four tree species with generalist small white flowers: *Hymenopus heteromorphus* (Benth.) Sothers and Prance var. *heteromorphus* (Chrysobalanaceae) (one tree, one season: trap sample) (Kirmse and Chaboo, 2020), *Matayba guianensis* Aubl. (Sapindaceae) (two trees, one season: trap sample), and *Tachigali guianensis* (Benth.) Zarucchi and Herend. (Fabaceae) (one tree, one season: trap sample) (Kirmse et al., 2003). *Hymenopus heteromorphus*, *M. guianensis*, and *T. guianensis* were mass-flowering, producing a very high number of flowers over a short period (Heinrich and Raven, 1972; Frankie, 1975). The fourth species, *Ocotea* aff. *amazonica* (six trees: trap sample), did not exhibit mass-flowering. The second group comprises tree species with flowers of other syndromes, such as *Balizia pedicellaris* (DC.) Barneby and J.W. Grimes (Fabaceae) (one tree, two seasons: trap sample), *Podocalyx loranthoides* (one tree, three seasons: combined trap and hand collection), and *Qualea paraensis* Ducke (Vochysiaceae) (one tree, one season: combined trap and hand collection).

3 Results

3.1 Diel activity of the beetle community

In total, 6,738 adult beetles were collected from 23 canopy-tree species. These beetles were assigned to 862 (morpho-)species belonging to 45 families. During the entire survey, I observed the activity of 535 beetle species (62.1%) representing 5,948 individuals (88.3%) in the canopy, while the activity of 327 species remained unknown (Figure 1). Of the 535 species with assigned diel activities, 198 (37%) were diurnal. In contrast, 281 beetle species (52.5%) were found to be active at night. In 56 beetle species (10.5%), I found both individuals active during the day and night. The 198 diurnal species comprise 1,983 individuals (33.3%), whereas the 281 nocturnal species include 2,024 individuals (34%). The proportion

of individuals representing indifferent species in the canopy sample was 32.6% (1,941 individuals).

Visitors to flowers and extrafloral nectaries were regularly found only during their phases of activity on their host trees. Commonly, these beetle guilds do not rest on their host trees. An exception were beetle species associated with dense inflorescences or infructescences of *Oenocarpus bacaba*. These beetles often remained inside the resources during both the day and night. In contrast to most flower and extrafloral nectary visitors, foliage feeders usually occur both day- and nighttime on their host trees. Among the leaf feeders, I found both strictly diurnal species (all Buprestidae) and species active during the day and night, such as a species of *Naupactus* Dejean (Entiminae).
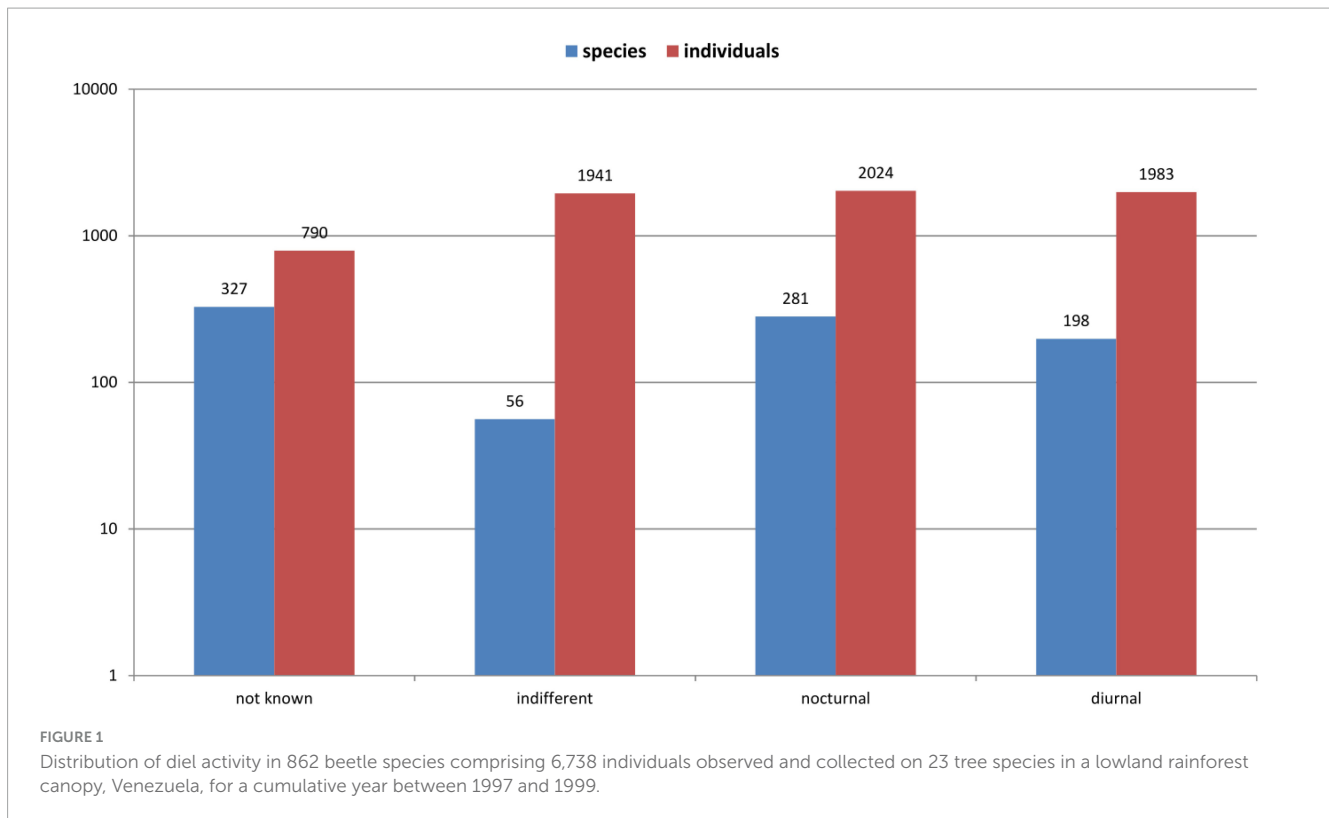
3.2 Diel activity of taxa

Of all identified genera comprising at least two species with observed activity ($n = 72$), species of 47 genera (65.3%) showed uniform diel activity in the canopy, whereas in 25 genera (34.7%) species showed both diurnal and nocturnal activity. Among the 11 well-observed beetle families comprising at least 10 species (Brentidae, Buprestidae, Cantharidae, Carabidae, Cerambycidae, Chrysomelidae, Curculionidae, Elateridae, Mordellidae, Scarabaeidae, and Tenebrionidae), Buprestidae showed clear diurnal activity, and Elateridae were found in general active during the night in the canopy. Carabidae (54 spp. nocturnal, 2 spp. diurnal, 1 sp. indifferent) and Tenebrionidae (17 spp. nocturnal, 1 sp. diurnal) were mainly nocturnal, whereas Mordellidae (14 spp. diurnal, 1 sp. nocturnal) were commonly diurnal. In contrast, Brentidae, Cantharidae, Cerambycidae, Chrysomelidae, Curculionidae, and Scarabaeidae did not exhibit uniform diel activity patterns among their respective species and genera. For instance, Chrysomelidae comprised 25 diurnal and 44 nocturnal species, Curculionidae comprised 53 diurnal and 59 nocturnal species, and Scarabaeidae nine diurnal and 20 nocturnal species.

Generalizing the diel activity in two beetle families and 11 genera, the beetle community collected on the 23 canopy-tree species comprised 568 species including 6,082 individuals. Of these 568 species, 215 (37.9%) were diurnal, whereas 298 (52.5%) showed nocturnal activity. Diurnal species comprised 2,055 individuals (33.8%), and nocturnal species 2,087 individuals (34.3%). Fifty-five species (9.7%) with 1,940 individuals (31.9%) remained indifferent.

3.3 Diel activity and diet

Of the 535 beetle species observed, diel activity was analyzed in relation to the plant diet commonly utilized in the canopy. A diet was assigned to 482 beetle species, comprising 242 nocturnal species (1,980 individuals), 185 diurnal species (1,969 individuals), and 55 indifferent species (1,937 individuals) (Figure 2). Among the diurnal species, visitors to small white flowers prevailed (128 spp., 69.2%; 1,327 individuals, 67.4%). They were followed by visitors to diverse flowers (36 spp., 19.5%; 440 individuals, 22.3%). Although indifferent species contained an almost equal proportion of individuals visiting small white flowers with a generalized

FIGURE 1
Distribution of diel activity in 862 beetle species comprising 6,738 individuals observed and collected on 23 tree species in a lowland rainforest canopy, Venezuela, for a cumulative year between 1997 and 1999.

morphology (1,335 individuals, 68.9%), they comprised only 16 species (29.1%). This group was followed by species that utilized diverse diets (15 spp., 27.3%; 226 individuals, 11.7%) and visitors to diverse flowers (10 spp., 18.2%; 181 individuals, 9.3%). In contrast, nocturnal beetle species were observed most often, utilizing more parts of the trees or other than flowers and extrafloral nectaries (66 spp., 27.3%; 705 individuals, 35.6%). These species with diverse diets were followed in similar proportions by species utilizing flowers and extrafloral nectaries (45 spp., 18.6%; 407 individuals, 20.6%), visitors to diverse flowers (44 spp., 18.2%; 478 individuals, 24.1%), visitors to small white flowers (40 spp., 16.5%; 227 individuals, 11.5%), and extrafloral nectary visitors (43 spp., 17.8%; 135 individuals, 6.8%).
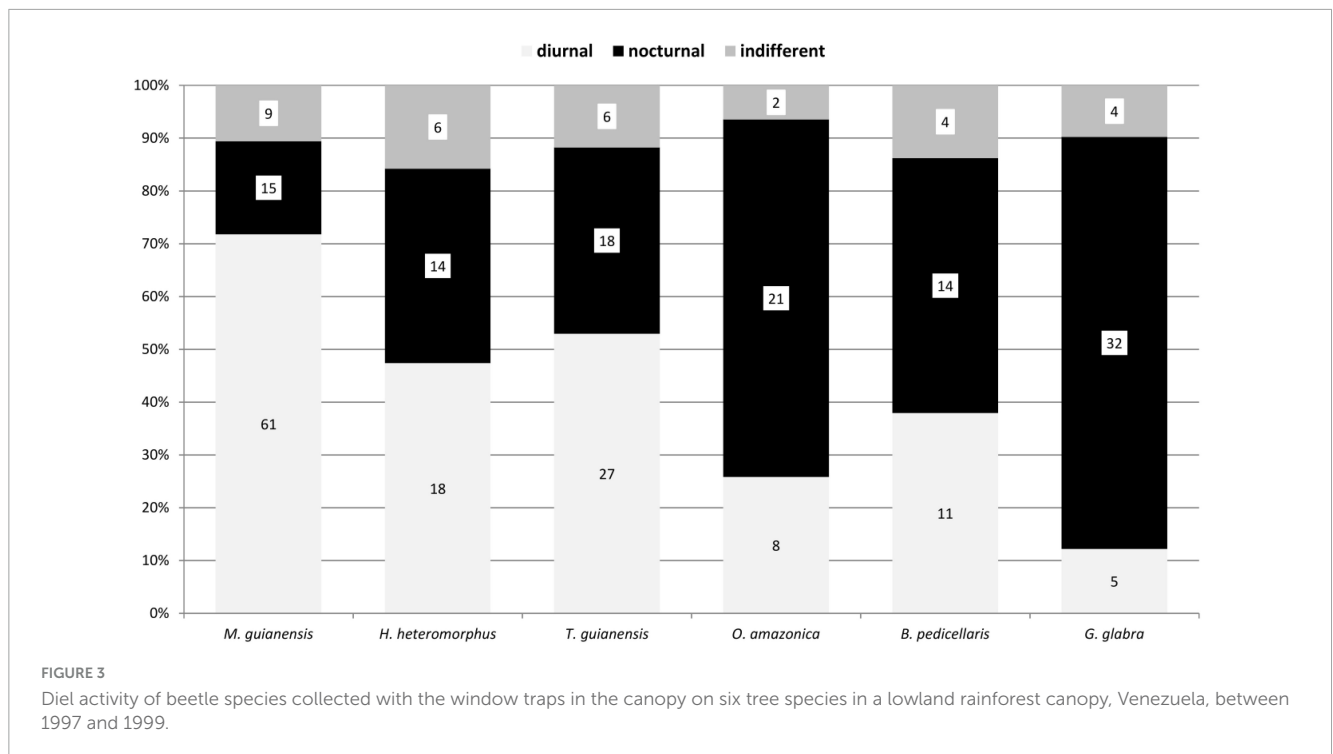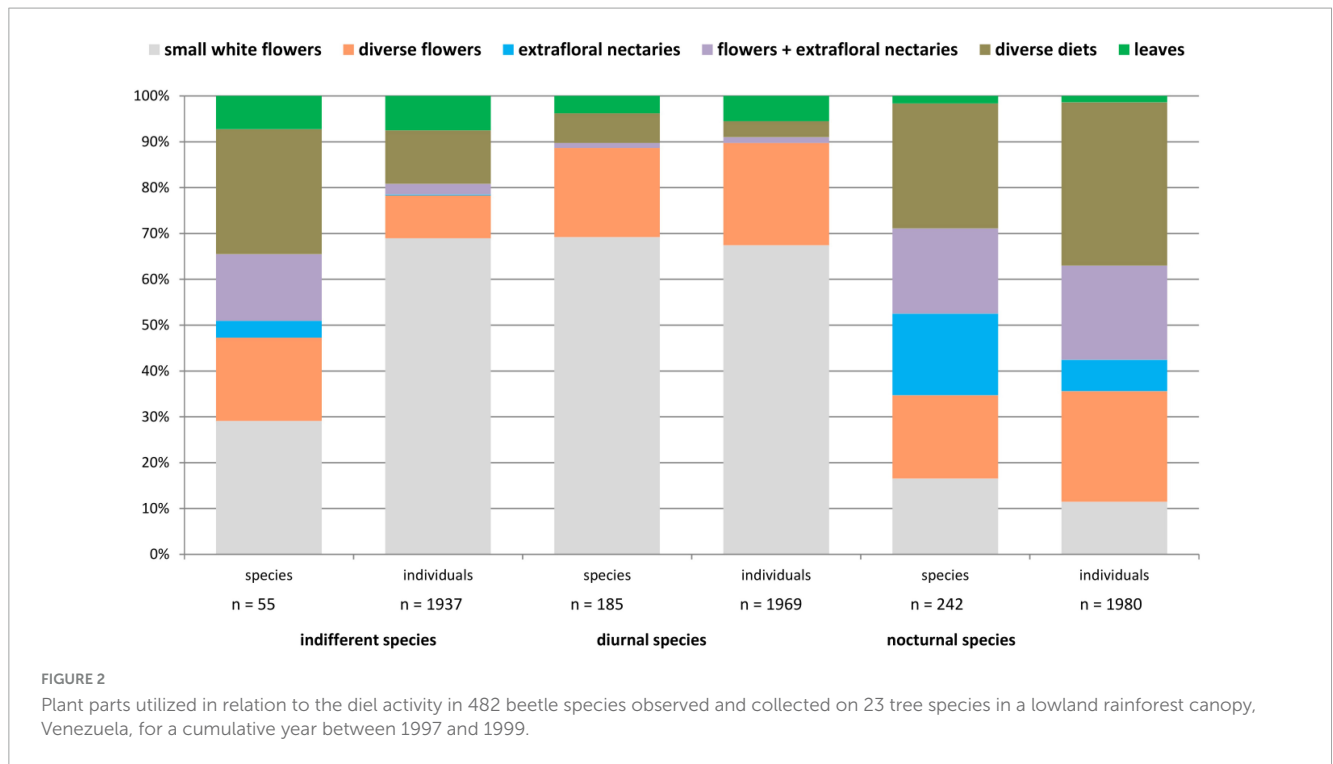
3.4 Diel activity and food resources

The diel activity of the beetle communities on the tree species varied, but showed distinct patterns associated with the phenological seasons and available food resources. Diurnal species were particularly represented in flowering trees (Figures 3–6). The highest proportion of diurnal flower visitors was trapped on the three mass-flowering tree species *H. heteromorphus* (47.4% of the species), *M. guianensis* (71.8% of the species), and *T. guianensis* (52.9% of the species). These three tree species also had the highest proportions of diurnal individuals. The other flowering tree species, *O.* aff. *amazonica*, *B. pedicellaris*, *P. loranthoides*, and *Q. paraensis*, attracted more nocturnal than diurnal species and individuals. The three year-aspect samples of *G. glabra*, *R. trichanthera*, and *S.* cf. *silvestris* contained approximately five times more nocturnal than diurnal species. The dominance of

nocturnal individuals in these tree species was expressed as at least three times higher numbers. The beetle communities collected on *L. hebantha* and *M. subarachnophylla* were observed exclusively during night feeding on extrafloral nectar secreted from emerging foliage for about three weeks.

4 Discussion

4.1 Assignment of diel activity

The assignment of diel activity to adult beetles in this canopy survey should be largely correct, as visitors to flowers and extrafloral nectaries were regularly found only during their phases of activity on their host trees. There are only a few exceptions for diurnal beetle species resting in the canopy of neighboring trees at night [e.g., *Macraspis festiva* Burmeister (Kirmse and Ratcliffe, 2019); *Tetraonyx* Latreille sp. 1 (Meloidae)]. In a few cases, the spotlight used to enable observations at night might have disturbed diurnal beetles resting in the canopy, possibly leading to a false assignment of diel activity. Resting on the host was observed by Rausher and Fowler (1979) in *Chauliognathus distinguendus* Waterhouse (Cantharidae), which spent the night in a quiescent state congregating on the leaves and inflorescences of a Polygonaceae in Costa Rica. Similarly, some nocturnal beetle species were quiescent inside dense inflorescences or inside closed flowers during the day, as observed by Listabarth (1992) in bactridine Arecaceae in Peru. The large proportion of indifferent beetles in this survey was mainly due to species associated with dense inflorescences or infructescences of *O. bacaba*. Among these

FIGURE 2
Plant parts utilized in relation to the diel activity in 482 beetle species observed and collected on 23 tree species in a lowland rainforest canopy, Venezuela, for a cumulative year between 1997 and 1999.

FIGURE 3
Diel activity of beetle species collected with the window traps in the canopy on six tree species in a lowland rainforest canopy, Venezuela, between 1997 and 1999.

beetle groups, clear differentiation between diurnal and nocturnal activity was not possible.

4.2 Habitat filtering

Gaston (2019) advised that ecologists are biased toward studying daytime phenomena. Owens et al. (2020) added that this is regrettable, because half of all insect species are nocturnal. This bias was avoided by collecting and observing adult beetles during the day and night on their host trees. I found that the proportions of nocturnal and diurnal individuals were balanced among the 23 canopy-tree species. In contrast to the Venezuelan study, Hernández-Camargo et al. (2017) found that most of the 648 beetle specimens collected from 26 families were active at night (59.87%) in a tropical deciduous forest in Mexico. Unlike the number of
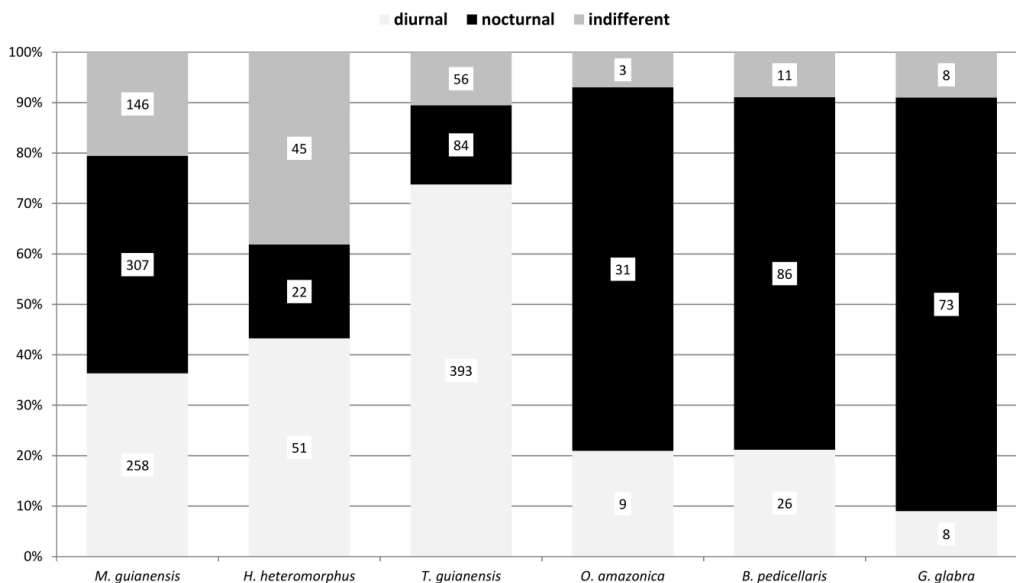
FIGURE 4
Diel activity of adult beetle individuals collected with the window traps in the canopy on six tree species in a lowland rainforest canopy, Venezuela, between 1997 and 1999.
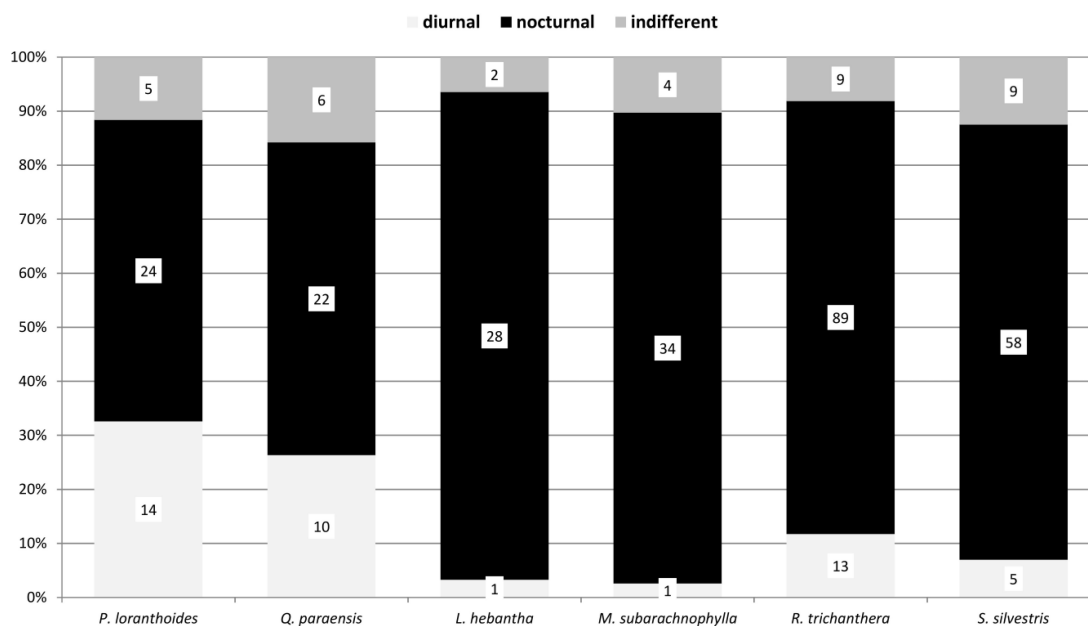

FIGURE 5
Diel activity of beetle species collected with hand and in the window traps in the canopy on six tree species in a lowland rainforest canopy, Venezuela, between 1997 and 1999.

individuals, the number of species encountering the Venezuelan canopy at night was with 52.5% higher than the 37% of beetle species that occur during the day. This suggests that more beetle species can cope with the canopy conditions at night. Nonetheless, Hernández-Camargo et al. (2017) collected a similar proportion of nocturnal (41.7%) and diurnal (41.2%) species among 202 beetle species in Mexico. Dealing with both hot and dry conditions in tree canopies during the day requires some kind of stress tolerance. In general, the considerable exchange between nocturnal and diurnal

beetle species occurring in the canopy may be largely attributed to the high fluctuations in relative humidity and air temperature by almost 10°C (Walsh, 1996; Szarzynski and Anhuf, 2001). In concordance with the Venezuelan study, Schowalter and Ganio (2003) observed a diurnal change in the presence and relative abundance of arthropods in one species of Cecropiaceae in Puerto Rico, with several taxa being more abundant at night.

Apart from dealing with the harsh microclimatic conditions at the interface between tree tops and the atmosphere, there are
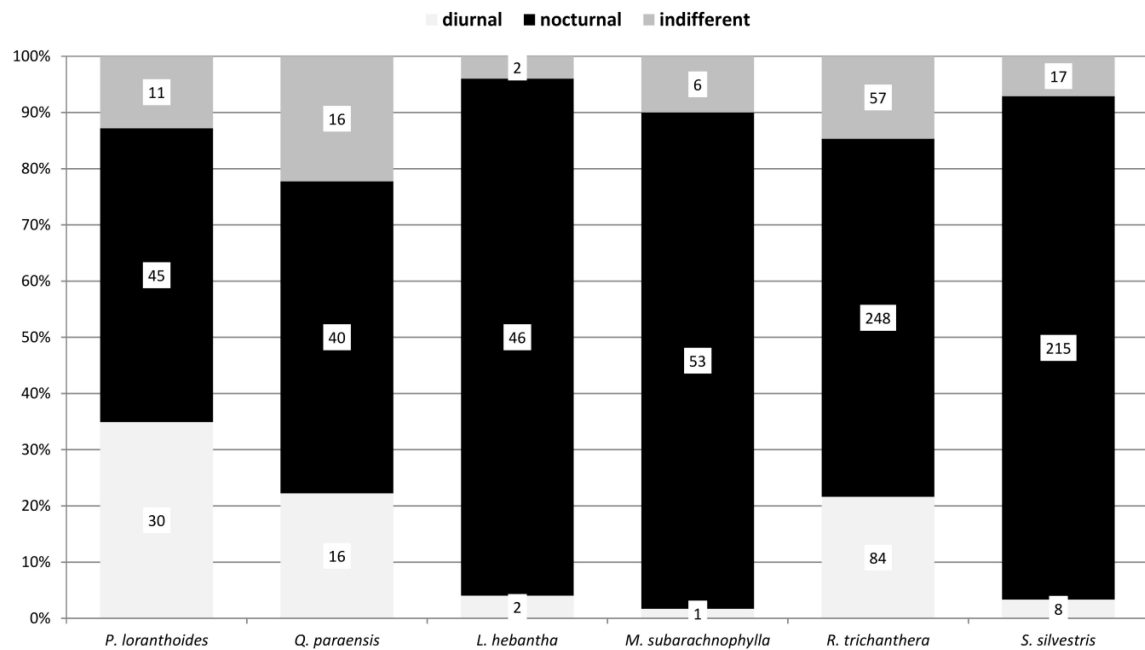
Diel activity of adult beetle individuals collected with hand and in the window traps in the canopy on six tree species in a lowland rainforest canopy, Venezuela, for a cumulative year between 1997 and 1999.

possibly many more factors that force the daily exchange of canopy beetles. For instance, predators can be attracted to aggregations of insects that feed on flowers (Wardhaugh et al., 2013). Ants represent the most abundant animal group in the canopy of tropical forests, and thus significantly influence the diversity, structure and dynamics of arboreal arthropod communities (Erwin, 1983; Floren and Linsenmair, 1994; Harada and Adis, 1998; Basset, 2001; Philpott and Armbrecht, 2006; Floren et al., 2014). Novotny et al. (1999) showed that ants were responsible for 77% of the predatory attacks and were three times stronger during the daytime. This may have forced the dominance of nocturnal beetle species in the Venezuelan canopy plot. Wagner (1999) found a significant correlation between chrysomelid beetle percentage and ant abundance in Central Africa. Other predatory arthropods like spiders or hymenopterans have naturally higher abundances and richness in lowland than in highland habitats (Lalisan et al., 2015).

4.3 Diel activity in relation to the taxon

Beetle species in most genera and some families show uniform diel activity in the canopy, suggesting that intrinsic preferences may cause diel activity patterns. In concordance with my survey, Gill et al. (2012) found that Mordellidae were diurnal, and Elateridae were nocturnal. Similarly, Carabidae showed predominantly nocturnal activity in a Mexican study (Hernández-Camargo et al., 2017). This Mexican study revealed almost only nocturnal Scarabaeidae and predominantly diurnal Chrysomelidae, in contrast to my findings. In a subtropical rainforest in Australia, canopy-associated species of Chrysomelidae and Scarabaeidae showed high activity during the night (Basset and Springate, 1992). The activity of Curculionidae was particularly high during the day,

whereas my dataset contained approximately as many diurnal and nocturnal Curculionidae.

However, the division of a dung-beetle community in Brazil into nocturnal and diurnal species is related to the coloring of species rather than to taxonomic classification (Hernandez, 2002). Furthermore, there is some evidence that some taxa show differences between geographic ranges. In the United Kingdom, 60% of carabid species are nocturnal and 20% diurnal (Luff, 1978), whereas in a tropical dry forest in Colombia, 80% of ground-dwelling Carabidae are nocturnal and 13.3% show both diurnal and nocturnal activity (Ariza et al., 2021). This may explain, in part, the differences between the results of several studies.

Often, the activity of beetles is not only diurnal or nocturnal but is also defined as distinct hours of the day. For instance, in Borneo, canopy dung beetle activity occurs at either midday or dawn-dusk (Davis et al., 1997). García-López et al. (2011) collected most scarab beetles in tropical forests during the first hours of the night. Most of the bioluminescent species investigated in Brazil are active during twilight and show short nocturnal activity after sunset (Viviani and Santos, 2012). In Brazil, *Cyclocephala putrida* Burmeister specimens started flying from 18:00 onward and were mostly collected from 20:00 to 22:00 h (Saldanha et al., 2020). However, I did not exactly discriminate the hours of activity due to the rather low abundances and collection of the 23 tree species at different times. Theoretically, this could have caused under-representation of beetles with short activity phases in the sample.

4.4 Diet and diel activity

Diel activity is associated with diet and food resources. Diurnal beetles predominantly visited small white flowers (Figure 2).

They dominated the communities of mass-flowering trees with small white flowers of a generalized morphology (**Figures 3**, **4**). In concordance, Ødegaard and Frame (2007) found beetle activity to be highest in the morning on two similar generalist blossoms of canopy trees in a Panamanian lowland forest. Similarly, Küchmeister et al. (1997) observed beetle visitors to *Euterpe* Mart. (Arecaceae), including Chrysomelidae, Curculionidae, and Staphylinidae only during the day. In a Malaysian Sapindaceae, visits ceased completely after 6 pm (Appanah, 1982). Although many beetle-pollinated plants flower during the day and night (Momose et al., 1998), other flower syndromes attracted more nocturnal than diurnal beetle species and individuals in the Venezuelan canopy plot. Accordingly, Sakai et al. (1999) found three times more beetles at night than during the day in one canopy tree in Malaysia. Species of *Annona* L. (Annonaceae) are usually visited by nocturnal beetles that escape during the day (Gottsberger, 1989). *Inga marginata* Willd. (Fabaceae) in Colombia, with a flower syndrome and phenology similar to that of *B. pedicellaris* was visited exclusively at night (Marin-Gomez et al., 2016).

The attraction of either diurnal or nocturnal beetles to different flowers may be due to several reasons. The production of floral nectar may be confined to the day or night, depending on diurnally or nocturnally active pollinator groups associated with a particular plant species (Cruden et al., 1983). The temporal patterns of nectar production dynamics (Pacini and Nepi, 2007) are usually linked to the foraging behavior of visiting animals (Nicolson, 2007). Additionally, plants may release different volatile blends during the day and night, which can attract or repel different visitor groups (De Moraes et al., 2001). In contrast to diurnal species, nocturnal beetles showed a broader spectrum of plant parts utilized in the Venezuelan assemblage (**Figure 2**). Moreover, many nocturnal beetles consumed extrafloral nectar, in contrast to diurnal beetles. For example, the extrafloral nectaries of *R. trichanthera* and *S. cf. silvestris* were visited by many nocturnal beetles (**Figures 5**, **6**; Kirmse, unpub. data). Heil et al. (2004) also found herbivorous beetles on extrafloral nectaries mostly at night. Extrafloral nectaries often exhibit strong variations in nectar flow during the day (O'Dowd, 1979). Nectar production may peak at a distinct time of day or night (Wickers, 1997; Heil et al., 2000; Raine et al., 2002; Heil and McKey, 2003). Elias et al. (1975) indicated that extrafloral nectaries in some plants have nectar production cycles that are correlated with the times of herbivores expected to be most active. Thus, the temporally restricted availability of resources may correspond to the visitor taxon.

5 Conclusion

The majority of beetle species (89.6%) showed either nocturnal or diurnal activity in the canopy of the studied Amazonian rainforest. According to their diel activity, most canopy-beetle species occupied the canopy temporally. This daily interchange may result in the findings of a few canopy specialists as well as the rapid recolonization of trees.

The fact that more than half of the beetle species observed were nocturnal implies that more beetle species can cope with the microclimatic conditions in the canopy during the night than during the day. Still, activity in the canopy is linked to the taxon, with several families active either during the day or night, indicating an intrinsic preference. In contrast, niche partitioning did not seem to play an important role in the canopy, as the beetle assemblages on a single tree species were dominated by diurnal or nocturnal beetles.

Although this beetle survey covered only a small proportion of the diversity of Amazonian tree species, the data suggest that studies on the diel activity of arboreal beetles should incorporate the identity of trees and their phenological seasons.

Data availability statement

The original contributions presented in this study are included in this article, further inquiries can be directed to the corresponding author.

Author contributions

SK: Conceptualization, Funding acquisition, Investigation, Writing – original draft, Writing – review & editing.

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Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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