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Tropical mountains as natural laboratories to study global changes: a long-term ecological research project in a megadiverse biodiversity hotspot

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Highlights

- We summarize a long-term ecological research in a megadiverse montane grassland
- We provide data on climate, soil, plant communities, plant mutualists and antagonists

Our goal is to integrate information into global mountain assessment networks

Abstract

Campo rupestre is a megadiverse vegetation mosaic dominating one of the world's geologically oldest tropical mountains. The campo rupestre hosts nearly 15% of Brazil's flora, with 40% of endemism in an area smaller than 1% of the national territory. Here, we summarize and explain the rationale underlying the long-term ecological research at Serra do Cipó (LTER-CRSC), in southeastern Brazil. The LTER-CRSC is a multi-taxa monitoring initiative focused on ecological patterns and processes along elevational gradients. We explain the standardized sampling methods of the LTER-CRSC and provide original data on climate, soil, and biodiversity along an elevational gradient. In our view, the LTER-CRSC offers a remarkable opportunity to improve predictions on how global change drivers affect biodiversity and ecosystem functioning in tropical, snow-free mountains. Our ultimate goal is to integrate the data from this study into a growing database from global mountain assessment networks and LTERs. We hope this initiative will stimulate collaboration and lead to further LTER sites being established in tropical mountains. Such efforts are needed as a basis for scientifically-based policy making, especially aimed at mitigating the effects of global change on tropical biodiversity and ecosystem functioning.

Key-words: elevation; Espinhaço Range; cerrado; long-term ecological research;

monitoring; rupestrian grassland

1. Introduction

Home to great biodiversity and high levels of endemism, mountains are especially vulnerable to global change drivers, particularly land-use changes and invasive species (Colwell et al., 2008; Hoorn et al., 2018). These impacts may trigger synergistic feedbacks, such as when climate and land use change interact, further increasing the risk of biological invasions (Pauchard et al., 2016). Yet, mountains provide food, water, shelter and secure essential ecosystem services for hundreds of millions of people in both lowlands and highlands (e.g., Körner, 2004, Fernandes et al., 2018; Hoorn et al., 2018; Payne et al., 2017). Mountains are also excellent systems for studying species responses to changing conditions, because climatic conditions change rapidly over short distances (Fernandes & Price 1988, Körner, 2004, Cowell et al. 2008). Thus, undergoing fast changes, being highly biodiverse, and providing many ecosystem services, mountains are important natural laboratories for long-term studies on global change and ecosystem resilience.

In some areas, elevation amplifies the rate of atmospheric warming, such that the temperature changes faster in high mountain environments than it does at lower elevations (Pepin et al., 2015). Throughout elevation gradients, temperature is regarded as a significant predictor of both plant and animal species diversity (e.g., Peters et al., 2016), but a decrease in land area at high altitudes is also an important driver of such changes (Körner, 2004). Many species that inhabit mountaintops are geographically restricted by lowland barriers or elevation differences (Steinbauer et al., 2016), and therefore, these organisms are among the most threatened in the Anthropocene.

Long-term ecological research (LTER) programs provide unique opportunities to study, on a global scale, the community dynamics of biodiverse ecosystems, including montane ecosystems, and how they are responding to global changes. The

establishment of permanent plots dedicated to the provision, documentation and monitoring of long-term data, with a time horizon of decades to centuries, is the most reliable way to track how global-change drivers are affecting natural ecosystems over long time series (Magurran et al., 2010; Mirtl et al., 2018), and to determine what strategies are needed to mitigate such impacts. Long-term biomonitoring in mountains is producing relevant data for predicting the effects of global change on species range shifts, local extinctions, alterations in species richness and composition, and rewiring of species interactions. Predicting trends in these phenomena can help establish thresholds and support the development of effective conservation and management policies (e.g., Colwell et al., 2008; Körner et al., 2017; Payne et al., 2017).

Considerable efforts have recently been made to establish mountain research networks, arising from the recognition that mountains are providers of ecosystem services essential to human well-being. Examples of such initiatives include the Mountain Research Initiative (MRI), the Global Mountain Biodiversity Assessment (GMBA), the Network for European Mountain Research (NEMOR), and Mountain Invasion Research Network (MIREN). However, existing mountain research networks show a strong geographic bias, with research largely concentrated in Europe and on geologically young mountains such as the Alps and the Andes.

Notwithstanding recent efforts, LTER studies are still scarce in the tropics, especially in tropical mountains (Mirtl et al., 2018) despite their disproportionately high biodiversity and degree of endemism (e.g., Barthlott et al. 1996; 2005; Kier et al. 2005; Hoorn et al., 2018). Tropical and ancient mountains have the potential to improve our theoretical understanding of the historical and contemporary factors driving biodiversity distribution and speciation (McDougall et al., 2011; Guo et al., 2018), because rates of

speciation, radiation, and extinction depend on long-term geological and climatic stability (e.g., Merckx et al., 2015; Schwery et al., 2015, Vidal-Jr et al. 2019).

The ancient Espinhaço Range in eastern Brazil is a major mountain range in South America, extending for 1,100 km SW-NE (Giulietti et al., 1997). In contrast to geologically young mountains such as the Andes (90-30 million years), some rocks of the Espinhaço Range date back to the Precambrian (Klein, 2005; Schaefer et al., 2016). Physical and chemical weathering have denudated the quartzite and granite rocks for over 1.8 billion years, resulting in a relatively low-elevation, snow-free mountain ranging from 800–2,100 m above sea level (Schaefer et al., 2016). The Espinhaço Range is bordered by the Caatinga (tropical seasonal dry vegetation) on its northern edge and by two biodiversity hotspots, the Atlantic Forest and the Cerrado, on its eastern and western slopes respectively (Morellato and Silveira, 2018). The core landscape is a vegetation mosaic dominated by *campo rupestre* — rupestrian grassland that characterizes the altitudes above 900 m — intermingled by quartzitic outcrops, surrounding forest patches, gallery forests, and mixed with Caatinga dry forests and Cerrado in the lower altitudes (Fernandes, 2016; Silveira et al., 2016).

The Espinhaço Range is internationally recognized as a UNESCO heritage site because of its biological, cultural, and historical values, and it represents one of the world's megadiversity and endemism centers (Giulietti et al., 1997; Fernandes, 2016). The mountaintop *campo rupestre* vegetation occupies less than 1% of the Brazilian territory, yet it hosts nearly 15% of the national flora (Silveira et al., 2016), suggesting that when considering total area, diversity in the Espinhaço Range may outnumber globally recognized centers of plant biodiversity such as the Cape Floristic Region and the Southwestern Australia Floristic Region (Hopper et al., 2016; Silveira et al., 2016).

Nearly 40% of *campo rupestre* species are endemic (ca. 2000 species), and many of those species are threatened with extinction (Martinelli and Moraes 2013).

Soils of *campo rupestre* are mostly sandy, shallow, with low water-holding capacity, and extremely impoverished, particularly in phosphorus (P; Oliveira et al., 2015; Silveira et al., 2016). Hence, most species evolved a stress-tolerant strategy (Negreiros et al., 2014) and have limited dispersal capacity (Silveira et al., 2016). Owing to a strong biological filter caused by impoverished soils, this ecosystem's native species have slow growth rates, and they are unlikely to out-compete invasive species on disturbed sites such as road margins (Barbosa et al., 2010; Fernandes et al., 2015) or to shift their distribution range upwards. Therefore, both biological invasion and climate changes pose pressing threats to the biodiversity and associated ecosystem services of the Espinhaço Range (Fernandes 2016; Fernandes et al., 2018).

Here, we synthesize the first phase (2010-2015) of the Long-term Ecological Research – Campo Rupestre Serra do Cipó (LTER-CRSC), focused on the *campo rupestre* at Serra do Cipó, southern Espinhaço Range. We also describe sampling protocols for ongoing subprojects included in the master project after 2015. The overarching goal of LTER-CRSC is to build a long-term transdisciplinary assessment of plant and animal communities along elevational gradients and across habitats (Fig. 1). First, we describe the history, characteristics, and rationale of the LTER-CRSC in the context of global change drivers and their impact on biodiversity and ecosystem services. Second, we define the experimental design and sampling protocols. Finally, we provide the metadata and the current long-term database on climate, soil, plant and insect communities, and mycorrhizal fungi, as well as data on underlying processes at the community and ecosystem-level (plant reproductive phenology, nutrient cycling, biological invasion, and regeneration ecology; Fig. 1; Table A1).

2. The history and rationale of the sampling protocols of the LTER-CRSC

LTER-CRSC was established at Serra do Cipó because of its unique geographic location within the Espinhaço Range (Fig. 2). The elevational gradient at Serra do Cipó was recognized decades ago as one the most important South American scenarios in which to develop eco-evolutionary studies (Fernandes and Price 1988, 1992). The focus of the LTER-CRSC project has been on plant community ecology and multi-taxa survey of associated fauna from *campo rupestre*, although functional aspects have gained attention in recent studies (e.g. Nunes et al. 2017). The campo rupestre sensu lato is defined as a montane, grassy-shrubby, fire-prone vegetation mosaic with rocky outcrops of quartzite, sandstone or ironstone along with sandy, stony and waterlogged grasslands (Silveira et al., 2016). With elevation-dependent warming, mountaintop biota may lose specific microhabitats (Scherrer and Körner 2011) in the short term, since they cannot move up to colder environments (Colwell et al., 2008) and cannot cross the valleys at lower elevations (Steinbauer et al., 2016, Pena et al. 2017). The key constraint on upward migration for most of species in *campo rupestre* is dispersal limitation: regardless of altitude, most endemic plants produce dry capsules that have no clear mechanism for seed dispersal and are typically dispersed a few centimeters away from the parent plant (Silveira et al. 2016), with secondary dispersers covering only short distances (Lima et al. 2013). Such strong dispersal limitation suggests mountaintop plants are unlikely to migrate upwards to cooler climates (MacLean and Beissinger, 2017; Morellato and Silveira, 2018).

Given that our main goal is to broadly understand how global change affects biodiversity along spatio-temporal dimensions, our sampling in the permanent plots includes plants, fungi, and many insects that are relevant to the plant life cycle and the

ecosystem (Fig. 1). We target taxa whose extinction or elevation shifts may result in cascading effects on the ecosystem. After briefly explaining the rationale for sampling each taxon/process, we provide details on the sampling protocols for the abiotic drivers of diversity (climate and soil data), the multi-taxa assessment (plants and their partners) and the communities and ecosystem processes. All necessary sampling permits were issued by Instituto Chico Mendes de Conservação da Biodiversidade, and all permits were requested for research in conservation units and private areas.

2.1 Field sampling sites of the Long-term Ecological Research – campo rupestre Serra do Cipó

Seven sites were selected along the elevational gradient of Serra do Cipó, covering the mosaic of vegetation types that occur across the mountain (Figure 2, Table 2). The sites range from 800 to 1400 m elevation, starting in the lowlands of Serra do Cipó National Park (Rio Cipó site: 800 m a.s.l.), covered by cerrado vegetation (Neotropical savanna), and ending at the Alto Palácio site (1400 m a.s.l.) in the National Park's highlands, dominated by *campo rupestre* (Table 2, Fig. 2). The five intermediate sites — Cedro (900 m a.s.l.), Serra Morena (1,000 m a.s.l.), Usina (1,100 m a.s.l.) Pedra do Elefante (1,200 m a.s.l.) and Quadrante 16 (1,300 m a.s.l.) — are on private land within the Morro da Pedreira Environmental Protection Area, the buffer zone surrounding Serra do Cipó National Park. Sampling was constrained to 1400 m because the decrease in land area at elevations above 1500 m restricts the number of potential sites to be sampled (Table 2).

Each site contained at least one linear transect and 13 plots of 10×10 m, which were spaced 10 m apart along a 250-m transect; the total sampling area at each site was

0.91 ha. All plant and invertebrate surveys were conducted within those plots, but details in the sampling protocols varied across taxa and are explained below.

2.1 Climatic data

To monitor the climatic dynamics, one full weather station (equipped with a solar powered Onset HOBO 1 U30 data-logger) was installed at each site. The stations collect data on 14 variables continually, at 5-minute intervals. The collection of weather data has been essential to capture microclimatic variation along the elevational gradient. Each station collects data on the following variables: air temperature, relative and absolute air humidity, global solar radiation, photosynthetically active radiation, atmospheric pressure, precipitation, soil humidity and temperature (at 5 and 20 cm depth), wind speed, wind direction, wind gust, and leaf wetness. All sensors and devices were set on 3-m-high towers, except for the soil temperature and humidity sensors, which were buried 5 and 20 cm deep, and the leaf wetness sensors, which were set 25 cm above ground. The air temperature probes were shielded from solar radiation.

2.2 Soil variables

Extensive periods of weathering, coupled with nutrient-poor parental rocks in *campo rupestre* (Schaefer et al., 2016), have resulted in extremely impoverished soils (Oliveira et al., 2015). Edaphic control of plant distribution should be especially important in landscapes with nutrient-poor soils (Negreiros et al. 2014, Hopper et al., 2016; Lambers et al. 2018, Mota et al., 2018). Furthermore, soil properties are of central relevance in determining competition outcomes of native versus invasive plant species (Barbosa et al., 2010), a matter that deserves attention because of its significant potential to influence management strategies to control invasive species.

LTER-CRSC soil sampling was conducted in the 13 plots along the elevational gradient (described above), between December 2010 and March 2011. From each plot, we obtained a 500-g composite sample by extracting surface soil (0-20 cm depth) from the four corners and the center of each plot. After collection, the soil samples were dried in open air and passed through 2-mm sieves. Soil chemical and texture analyses were done at the Soil Analysis Laboratory at the Institute of Agrarian Sciences, Federal University of Minas Gerais, according to the EMBRAPA (1997) protocol. The following attributes were evaluated: pH in water (pH); levels of potassium (K) by flame photometry; phosphorus (P-Mehlich) by colorimetry; and calcium (Ca) and magnesium (Mg) by atomic absorption spectrophotometry. We calculated the sum of bases (SB), cation-exchange capacity at pH 7 (CECpH7), effective cation-exchange capacity (CECe), base saturation (V%) and aluminum (Al) saturation (m%), and analyzed the remaining P using anion-exchange resin. Soil organic matter (SOM) was determined using humid oxidation with potassium dichromate in a hot sulfurous environment. The excess dichromate was titrated with a standard ferrous ammonium sulfate solution (Mohr's salt), following EMBRAPA (1997). To determine the proportion of sand, silt and clay, we performed granulometric analysis using the pipette method based on Stokes' law describing sedimentation of particles, with a solution of sodium hexametaphosphate buffered with sodium carbonate for the total dispersion of particles. All data are expressed per unit of soil dry matter.

2.3 Plant communities and vegetation

The elevation gradient of the LTER-CRSC study area described here comprises both cerrado vegetation in the lowlands and *campo rupestre* in the highlands. There are marked changes in species composition, vegetation structure, and frequency of life-

forms along the elevation gradient. Beta diversity among sites represents 93% of the total diversity, and species turnover is, numerically, the primary mechanism that determines the beta diversity (Mota et al., 2018).

From 2011 to 2015, we conducted sampling between January and July, covering both the rainy and dry seasons. Within each plot across the seven elevation sites (described above), we sampled and identified all woody and rosette species with a diameter ≥ 1 cm at soil level. Plant material collected from each species was deposited at the Montes Claros Herbarium (MCMG), Montes Claros, Minas Gerais State, Brazil. Plants were identified through reference to the literature, consultation with experts, and comparison with voucher specimens from collections at the Federal University of Minas Gerais (BHCB Herbarium) and the University of São Paulo (SPF Herbarium).

2.4 Soil seed banks

The soil seed bank is a key part of a plant community's regeneration process (Garwood, 1989), but rare are the studies on the regenerative potential of the soil seed bank in *campo rupestre* (Medina and Fernandes, 2007). We sampled the seed bank in four periods — July 2014 (dry season), February 2015 (wet season), September 2015 (dry season), and February 2016 (wet season) — at the same elevations and plots as the vegetation sampling. In each plot, samples of superficial litter and soil were collected at depths of 0–5 cm (Luz et al., 2018). The germination method (Brown, 1992) was used to evaluate the seed bank. The litter and soil samples from each plot were divided into two and placed in greenhouses under two light conditions (direct light and 50% shade) in order to assess species germination. Samples were monitored weekly, for 12 weeks, by counting and morphotyping all individuals that germinated. Trays with sterilized sand served as controls for allochthonous seed arrival. Identification of the botanical

material was performed with the assistance of experts and specialized botanic literature, and plant material was deposited in the MCMG herbarium.

2.5 Mycorrhizal fungi

Mycorrhizas are structures arising from mutualistic interactions between plants and fungi. At a single site of *campo rupestre* at Serra do Cipó, Carvalho et al. (2012) reported 49 species of arbuscular mycorrhizal fungi (AMF), which corresponded to 23% of the global AMF diversity. Coutinho et al. (2015) reported an additional 14 species likely new to science and another nine new records for Brazil. However, in the severely P-impoverished soils in *campo rupestre*, AMF probably plays only a minor role in P acquisition (Oliveira et al., 2015) while playing a far more critical role in boosting plant defense (Lambers et al., 2018). In such cases, plants are not colonized by AMF but instead evolved root specializations, such as dauciform roots that release carboxylates in the soil, solubilizing P (Oliveira et al., 2015). Therefore, these data suggest that the functional role of AMF in *campo rupestre* is related to plant defense rather than P acquisition (Zemunik et al., 2018).

We sampled mycorrhizal fungi, in February and March of 2011, from each plot of each site along the elevation gradient. At each elevation, five soil samples were collected (one sample from each corner and one from the center) from the surface layer (0-0.2 m depth) within each plot. These samples were combined and homogenized to create a single mixed sample per plot (total n=91).

In each sample, AMF spores were extracted from the soil using the wet sieving technique, with 50 g of soil and 425- and 53-µm sieves, followed by centrifugation in a sucrose gradient (50%) (Jenkins 1964). Spores were counted using a stereomicroscope, separated into morphospecies, and then crushed under a coverslip in a drop of either

polyvinyl alcohol lactoglycerol (PVLG) or 1:1 (v/v) PVLG+Melzer's reagent (Morton et al., 1993) to visualize their walls. Identification of AMF species was based on the morphological traits of spores (see details in Coutinho et al., 2015).

2.6 Bees

Bees are the main pollinators in *campo rupestre* (Carstensen et al., 2016; Silveira et al., 2016). Orchid bees (Hymenoptera: Apidae: Euglossini) are a primarily Neotropical clade of bees including five genera and more than 240 species (Moure et al., 2007). Orchid bees are the pollinators of more than 200 plant genera (Ramírez et al., 2002). Although the group is more diverse in forests (Nemésio and Silveira, 2007), it is also species-rich in open vegetation types, where the bees deliver essential pollination services (Antonini et al., 2016). The Euglossini of open vegetation fly over long distances and can pollinate a broad diversity of plants (Ramírez et al., 2002).

Males of Euglossini were sampled at the end of the rainy (April) and dry (September) seasons of 2017. Bee traps (details in Antonini et al., 2016) baited with synthetic odors were used in the sampling protocol. At each site, we installed nine traps of each bait (benzyl acetate, beta-ionone, cineole, methyl cinnamate, eugenol, methyl salicylate, and vanillin), totaling 63 traps per site. The traps were set 1.5 m above ground and a minimum of 2 m apart, either hung on standing vegetation or supported by sticks where vegetation was insufficient.

Baits were renewed in the morning (08:00 h), and traps remained in the field for 48 h. Specimens were removed from the traps at 16:00 h. After collection, the bees were frozen, taken to the lab and mounted for identification. All material was deposited in duplicate at the Laboratório de Ecologia Evolutiva e Biodiversidade, Federal University of Minas Gerais.

2.7 Butterflies

Butterflies have been focal organisms in the search for understanding of the biological and ecological factors regulating species distribution and community-level evolutionary processes, including those affecting vegetation (Didham et al., 2007; Basset et al., 2013). In addition to their importance in pollination (Carstensen et al 2016), butterflies represent a group with relevance to the plant community because the caterpillars of most species have specialized diets (Barrios et al., 2016; Jain et al., 2016).

To provide an estimate of the butterfly diversity and changes along the elevational gradient, we focused on nectarivorous and frugivorous butterflies. Sampling was conducted in January, April, July and October 2012, and in January, May, August and October 2013, thus encompassing the different seasons of the year. The sampling of nectarivorous butterflies involved the establishment of three 250 m-long transects, 500 m apart, at each of the seven sites. Two experts, carrying entomological nets, searched for individuals during three 2-hour periods: 08:00 to 10:00, 11:00 to 13:00, and 14:00 to 16:00.

Fruit-feeding butterflies were sampled using Van-Someren Rydon traps baited with fermented banana and sugar cane juice. In each site, we set up three 500-m transects and placed four traps, 50 m apart, in each transect. Traps were settled in the first day and checked daily for three consecutive days, for a total sample period of four days.

The sampled butterflies were identified with the aid of guides and specialists. All sampled material was deposited in the Zoology Museum of the Universidade de São

Paulo (MZUSP), Entomological Collection at the Universidade Federal do Paraná and the Laboratório de Ecologia Evolutiva e Biodiversidade.

2.8 Dung beetles

Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) represent a diverse and abundant group of ecologically relevant terrestrial insects. Dung beetles affect plant ecology and ecosystem functions through numerous processes, such as secondary seed dispersal, soil nutrient enrichment and aeration (Andresen, 2005; Braga et al., 2013), and even as natural enemies of leaf-cutting ants (Silveira et al., 2006). A primary ecological function provided by the dung beetle is the moderation of nutrient cycling in terrestrial ecosystems (Nichols et al., 2008; Slade et al., 2011). Using dung beetles as a bioindicator of the environmental conditions of *campo rupestre* contributes to our understanding of ecological processes such as dispersal, community assembly, and nutrient cycling (Nunes et al., 2018).

Dung beetles were sampled along the elevational gradient on seven occasions: at the end of the dry season in September 2013 and 2014; at the beginning of the rainy season in December 2013 and 2014; at the end of the rainy season in March 2014 and 2015; and at the beginning of the dry season in June 2014. To quantify dung beetle species richness, abundance, and biomass, we used baited pitfall traps. Traps were 9 cm deep and 15 cm in diameter, contained 250 ml of a salt and detergent solution, and were baited with 25 g of fresh human feces. Each trap was left in the field for 48 h, after which the beetles were collected, preserved and transported to the laboratory, where all captured individuals were identified to the lowest possible taxonomic level. We used an identification key to the genera and subgenera and the associated taxonomic literature cited in the identification of New World species of Scarabaeinae (Vaz-de-Mello et al.,

2011). All sampled material is deposited in duplicate at the Laboratório de Ecologia de Insetos at the Federal University of Minas Gerais.

2.9 Termites

Termites are considered ecosystem engineers, altering soil composition and structure and playing a fundamental role in nutrient cycling (Lavelle et al., 2006). Due to their sensitivity to moisture and temperature (Davies et al., 2015) and vegetation structure (Gillison et al., 2013), termites have been used in studies that investigate the influence of environmental factors and disturbance on community structure (e.g., Bourguignon et al., 2015).

Termites were sampled across the elevational gradient, in March 2012 (end of rainy season), using a collection protocol adapted from Jones and Eggleton (2000). In every section of each transect, a total of one person-hour was spent searching for termites across all microhabitats: leaf litter, inside and beneath dead wood and rocks, in nests on the ground, and on vegetation up to 2 m in height. We also dug one soil sample (10 x 10 x 10 cm) per section and inspected them for termites. All termites were stored in vials containing 80% ethanol and labeled accordingly. Termite identification was conducted by R. Constantino at the University of Brasília, where voucher specimens were deposited in the termite collection. Duplicates were deposited at the Federal University of Viçosa.

2.10 Ants

Ants (Hymenoptera: Formicidae) are a dominant component of terrestrial biomes worldwide. They are considered excellent bioindicators because they are highly abundant, diverse, and have a wide geographical distribution (Underwood and Fisher,

2006). However, little is known about their distribution patterns in tropical mountains, especially in *campo rupestre* (Costa et al., 2015). Ants interact as plant mutualists or antagonists, thus mediating many ecosystem functions and processes (Dell et al., 2014; Del Toro et al., 2015, Costa et al., 2016).

Ants were sampled over four years, during four periods in each year, at the beginning and end of the rainy and dry seasons. We distributed our sampling sites along the elevational gradient, installing three 250-m transects, which were spaced at least 250 m apart. Within each transect, we set five traps, spaced 50 m apart (15 traps per sampling site, 105 in total). To quantify ant species richness, we used baited pitfall traps. Traps were 9 cm deep, 15 cm in diameter, and contained 250 ml of a salt and detergent solution. Each trap was left in the field for 48 hours, after which the ants were collected, preserved and transported to the laboratory, where all individuals were identified to the lowest possible taxonomic level. All sampled material was deposited in duplicate at the Laboratório de Ecologia de Insetos, Federal University of Minas Gerais.

2.11 Aquatic insects and leaf breakdown

Riparian plants supply streams with nutrients, buffer daily temperature and light fluctuations, filter runoff, provide wood debris for physical habitat structure, and produce organic detritus that becomes an energy source for local food webs (Callisto et al., 2012). The allochthonous input of leaf detritus from riparian vegetation is the main energy source for the aquatic metabolism (as heterotrophic ecosystems). The decomposition of terrestrial plant litter is one of the most vital ecosystem processes in the biosphere and is particularly sensitive to climate change (Boyero et al., 2011b). Although most terrestrial plant biomass is decomposed on land, recent estimates have shown that decomposition in inland waters contributes significantly to the global carbon

cycle as a result of rapid metabolic rates, facilitated by constant water availability and nutrient supply. Thus, riparian plant decomposition in streams is relevant to global biogeochemistry, with possible positive feedback in a global climate change scenario (Boyero et al., 2011a).

In the Espinhaço Range, waters are nutrient-poor due to the extremely impoverished soils, which in turn limits aquatic productivity and the contribution of microbial leaf breakdown. In general, *campo rupestre* species produce scleromorphic leaves that have low fungal biomass when decomposing in streams (Gonçalves et al., 2006). A recent finding is that riparian plant litter quality increases with latitude, and that riparian *campo rupestre* species produce among the lowest litter quality worldwide (Boyero et al., 2017). High leaf scleromorphy limits microbial colonization and activity and slows down leaf litter decomposition (Gonçalves et al., 2006; Moretti et al., 2007). Therefore, leaf detritus would need to remain submersed for longer to be colonized by shredder invertebrates (Ligeiro et al., 2010).

Leaf shredders are species-poor and less abundant in tropical streams than in streams at higher latitudes (Boyero et al., 2012); consequently, species loss in tropical streams is more likely to lead to loss of ecosystem functions. Some of the shredder species are close to their thermal maxima in the tropics, which makes them more sensitive to climate warming (Boyero et al., 2012).

To evaluate how the elevational gradient influences species richness and spatiotemporal beta diversity of aquatic insects, samples were collected from cobbles, gravel, and leaf litter deposits in different streams nearest to the LTER-CRSC sites. Afterwards, leaf-breakdown experiments were performed using a global protocol for experiments on leaves from native, alien and global reference plant species (Boyero et al., 2015, 2017). Leaves were placed inside coarse and fine nylon litter bags, incubated

in streams for 30, 60 or 90 days, and then retrieved to be weighed in the laboratory. Additionally, water nutrient concentrations, physical and chemical traits, and leaf quality were analyzed in laboratory to test the importance of nutrients, microorganisms and detritivorous invertebrates on leaf breakdown (Boyero et al., 2011a; 2011b). To evaluate the risk of predation for larvae of *Phylloicus angustior* (Trichoptera: Calamoceratidae) during leaf-litter consumption and case-building, we performed laboratory experiments under controlled daylight and temperature conditions. Different native and alien plant species were tested to assess the importance of this typical Neotropical shredder in nutrient cycling in *campo rupestre*. All sampled material was deposited in duplicate at the Benthic Macroinvertebrates Reference Collection at the Instituto de Ciências Biológicas, Federal University of Minas Gerais.

2.12 Invasive species

Roads have a significant impact on global mountain ecosystems, causing disturbances, changing species compositions, fragmenting habitats, changing the hydrology, soil ecology, and nutrient availability, altering the microclimate, and funneling invasion into the most pristine environments (Lembrechts et al., 2017). Introduction of invasive species potentially leads to new belowground and aboveground interactions (Pauchard et al., 2016), leading to the rewiring of ecological networks.

To understand the effects of environmental changes on the biological invasion dynamics, we focused on the elevation limits and species range of non-native species (Seipel et al., 2016). In the pristine *campo rupestre*, the spread of invasive species is strongly limited by nutrient availability. In contrast to the conservative resource strategy typical of native species (Reich, 2014), invasive species have often evolved an acquisitive strategy and therefore only occur along roadsides where resource availability

is relatively high (Barbosa et al., 2010). Accordingly, invasive plants were not sampled at the same sites as other vegetation, along the elevational gradient, but were instead sampled from 17 sites along highway MG-010. The sampling extended from km 100 (W43° 35' 55", S19° 17' 35.4") to km 128 (W 43° 34' 00", S 19° 17' 25"), covering an elevational range from 850 m to nearly 1400 m. Four 10 x 10-m transects were installed perpendicular to the highway. Samples were collected and identified by specialists in 2017. Abundance was estimated for all invasive species.

2.13 Plant reproductive phenology

The study of recurrent life-cycle events in plants and animals provides fundamental information about the drivers of plant growth and reproduction and about the likely responses to global change drivers and their consequences, especially in terms of plant-animal interactions (Memmott et al., 2007; Morellato et al., 2016; Thackeray et al., 2016). We aimed to understand the dynamics of the reproductive phenology of *campo rupestre* along the elevational gradient described above. Specifically, we asked whether reproductive phenology is seasonal, and whether phenological patterns differ among elevations; we also sought to identify the main environmental drivers (Streher et al., 2017) of flowering and fruiting phenology. Ultimately, our results would allow us to draw preliminary conclusions regarding the potential effects of climate change on plant phenology and plant-animal interactions.

We observed the phenology at six of the seven sites sampled by the LTER-CRSC (Rocha et al., 2016). We excluded the Serra Morena site because the vegetation was similar to other sites and vegetation types distributed over the elevational gradient, as described below. At each study site, we conducted the phenological observations in 13 plots set along a linear transect, each plot measuring 10×2 m and spaced 10 m

apart, as per the LTER-CRSC design. within the plots, all rosettes, herbs, shrubs, and trees larger than 1 cm diameter at soil level were sampled, tagged and observed monthly, from August 2012 to December 2014, to record changes in reproductive phenology.

We recorded the presence or absence of flowering (flower buds and open flowers) and fruiting (unripe and ripe fruits) events. During the observations, newcomers were included in the survey. Some individuals died or were lost during the study. Two fire events were recorded during the study period: October 10, 2012, on the RC site; and October 10–14, 2014, when a more significant fire from burned at the CE, PE, Q16, and AP sites. Vouchers of plant species, during their reproductive phase, were collected near the plots at all study sites and were deposited in the Herbaria HRCB (Herbarium Rioclarense — São Paulo State University at Rio Claro), with duplicates at BHCB.

We also installed digital cameras (phenocams) at each climatic station, in October 2014, to collect data on leafing phenology and to monitor the dynamics of leaf out, growth and senescence along the elevational gradient; the cameras were programmed to continually capture photographs on an hourly or daily basis (Alberton et al., 2017). With this data, we aim to determine the extent of the growing season across the elevational gradient, the environmental drivers of leaf exchange, and the vegetation's responses to anthropogenic and natural disturbances such as fires.

3. Perspectives and conclusions

LTERs in tropical sites, particularly in tropical mountains, provide unprecedented opportunities to monitor, detect, and mitigate effects of climate changes and other human-induced disturbances. Because the drivers of biodiversity can vary

geographically (Magurran et al., 2010), data obtained from LTER in temperate mountains cannot be extrapolated to tropical sites. The LTER-CRSC, however, offers multiple opportunities to advance our understanding on how global change drivers affect biodiversity and ecosystem services in tropical mountains.

First, the LTER-CRSC has allowed us to gain knowledge about the natural history of an overlooked ecosystem. Our multi-taxa approach has brought to light new species, novel species interactions, and insights into the assembly of natural communities across scales (e.g., Carstensen et al., 2016, 2018, Mota et al. 2018, Nunes et al. 2017, Fernandes et al. 2018). Gaining knowledge on taxonomic diversity and natural history is a first step in addressing questions on functional and phylogenetic diversity, and in examining turnover in interaction networks along elevation gradients. Second, our long-term dataset on plants, animals and fungi will provide a baseline for addressing temporal changes in biodiversity, which in turn can support efforts to reduce the rate of biodiversity loss (Magurran et al., 2010). With temporally accumulated data in hand, we will be able to monitor temporal beta diversity and detect natural and atypical variations in species composition of meta-communities. Third, long-term datasets on climate and soil will allow the development of mechanistic understanding of the drivers of temporal biodiversity change. Species distribution patterns along elevational gradients at Serra do Cipó were documented decades ago (e.g. Fernandes & Price 1988, 1992), but mechanisms shaping these patterns are still contentious. Fourth, the long-term assessment of biodiversity distribution along elevational gradients will allow us to track, for the first time, elevation range shifts across a wide range of plant and animal taxa in tropical mountains (see MacLean and Beissinger, 2017; Rumpf et al., 2018). Thus, our long-term assessment will support the development of spatially explicit models of environmental suitability for the taxa studied against the prospect of

temperature increase and change in rainfall. Furthermore, these models can be extended throughout the Espinhaço mountain range and, potentially, applied to other ancient, unglaciated landscapes. Finally, our permanent plots will allow us to detect early warning signs of tipping points — critical thresholds at which a tiny perturbation can qualitatively alter the state or development of a system (Lenton et al., 2008) — and propose mitigation measures. Tipping points have been examined in the Amazon forest and the cerrado (Hirota et al., 2011) but are virtually unknown for montane grasslands. In our particular system, main stressors (Harley et al., 2017) include increasing fire frequency, increasing temperature and decreasing rainfall (IPCC, 2014).

The 2015–2020 LTER-CRSC continues its bio-climatic monitoring, now expanding to a more comprehensive plant survey that includes grasses, forbs, and herbs. We are also investigating additional dimensions of biodiversity, such as functional and phylogenetic diversity along the elevation gradient, mutualistic interactions across elevation, and the spatio-temporal drivers of change in species diversity and distribution. These findings will enable us to implement species–habitat networks to improve the efficacy of landscape management (Marini et al. 2019).

Mountain biodiversity research is an exciting and growing area of investigation, and we anticipate that our paper will galvanize future collaborations, provide the needed fuel for implementation of additional LTER sites in tropical mountains, and ultimately result in science-based conservation policy to mitigate the effects of global change on biodiversity in tropical montane ecosystems.

Author contribution

FAOS - Conceptualization, Methodology, Writing - original draft

GWF - Conceptualization, Data curation, Funding acquisition, Methodology, Project administration, Writing - review & editing
MB - Conceptualization, Data curation, Writing - review & editing
WB - Conceptualization, Data curation, Writing - review & editing
MC - Conceptualization, Data curation, Writing - review & editing
DRM - Data curation, Writing - review & editing
LPCM - Conceptualization, Data curation, Writing - review & editing
FSN - Conceptualization, Data curation, Funding acquisition, Project administration,
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YRFN - Conceptualization, Data curation, Writing - review & editing
RRS - Conceptualization, Data curation, Writing - review & editing

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Figure legends

Figure 1. Conceptual framework showing the multidisciplinary approach of the plantcentered component of LTER-CRSC. The drivers (grey rectangles) of different processes across a plant's life cycle (white circles) may permeate ecological scales, ranging from population to ecosystem levels.

Figure 2. The original distribution of the *campo rupestre* vegetation in Minas Gerais, southeastern Brazil (A), and the geographic distribution of the sampling sites of the LTER-CRSC at Serra do Cipó (B). Predictions of the variation in abiotic variables that drive key ecological processes and physiognomy variation along the elevational gradient (C).

Fig 1



Fig 2



Table 1. Details of the sampling period and target abiotic and multi-taxa sampled in each of the subprojects within the Long-Term Ecological Research of *campo rupestre* of Serra do Cipó (LTER-CRSC), southeastern Brazil, divided by phase 1 (2010-2015) and phase 2 (2016-2020). Each subproject has implications to understand plant ecology at the population, community, or ecosystem level. The original metadata and data are provided in the Supplementary Material (Table A1).

Subproje	Sampling period		Sampling interval	Coverag		
cts				Populat	e	Ecosyst
				ion	Commu	em
					nity	
	Phase	Phase	/	$\mathbf{\hat{\mathbf{N}}}$		
	1	2				
Climate	2011-	2016-	Hour		X	X
	2015	prese				
		nt				
Soil	2010-	2018	7-10 yr		Х	Х
	2011					
Plants	2011-	2016-	2 years		Х	Х
	2015	prese				
		nt				
Seed	2014-	2016-	2 years			
banks	2015	prese				
		nt				
Mycorrhi	2011	-	To be sampled		Х	X
zae						

Bees	-	2017	To be sampled		Х	
Butterflie	2012-	2016-	Quarterly/2 years		Х	
S	2013	prese				
		nt				
Ants	2011-	2016-	Quarterly/2 years		Х	
	2014	prese				
		nt				
Dung	2013-	2016-	Quarterly/2 years		x	x
Beetles	2015	prese				
		nt				
Termites	2012	-	To be sampled		Х	Х
Aquatic	-	2017	Dry season	x	Х	Х
insects						
Reproduc	2012-	-	Monthly	х	Х	
tive	2014					
phenolog						
у						
Leaf	2014-	2016-	Daily	х	X	X
phenolog	2015	prese				
у		nt				
Invasive	-	2017	2 years	X	X	X
species						

Site	Vegetatio	Terrain	Elevat	Site	Availab	Coordinates
Name	n		ion		le area	(lat/long)
(acro	cover				(km ²)	
nym)						
Rio Cipó	Cerrado	Onen land	821 m	Nationa	29.78	19° 21' 26.82" S,
(RC)		Open land		l Park		43° 36' 26.46" W
Usina (US)	Campo	Hillside/str	977 m	Private	16.92	19° 16' 8.40" S, 43°
	rupestre	eamside		area		36' 21.06" W
Serra	campo		1000	Private	28.84	19° 15' 41.16" S,
Morena	rupestre	Open land	m	area		43° 35' 8.34" W
(SM)						
Cedro (CE)	campo	Open land	1101	Private	39.52	19° 13' 47.64" S,
	rupestre	Open land	m	area		43° 34' 41.28" W
Pedra do	campo		1255	Private	36.55	19° 17' 29.94" S,
Elefante	rupestre	Hillside	m	area		43° 33' 29.28" W
(PE)						
Quadrante	campo	On an lond	1303	Private	26.02	19° 17' 46.98" S,
16 (Q16)	rupestre	Open land	m	area		43° 35' 32.10" W
Alto Palácio	сатро	Open land	1420	Nationa	5.69	19° 16' 0.18" S, 43°
(AP)	rupestre		m	l Park		32' 6.18" W

Table 2. The seven permanent study sites of LTER-CRSC set up in the elevationalgradient at Serra do Cipó (see also map in Fig. 1). Coordinates in datum WGS84.