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Conversion of Andean montane forests into plantations: Effects on soil characteristics, microorganisms, and microarthropods

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Abstract

Tropical montane forests in the Andes are subjected to deforestation and subsequent transformation into pastures. Abandoned pastures are frequently reforested by planting monoculture timber plantations, resulting in reduced aboveground diversity and changes in soil characteristics compared to primary forests. In this study, we evaluated differences in soil properties (litter layer thickness, pH, water content, and C-to-N ratio) between degraded primary montane forest and monoculture pine (*Pinus patula*) and alder (*Alnus acuminata)* plantations and their effects on density, diversity, and community structure of litter and soil-living mesofauna, with focus on oribatid mites (Acariformes). The study was performed in a montane region in the southern Ecuadorian Andes (2,000–2,600 m a.s.l.). C-to-N ratios in the litter and upper 5 cm soil layer were higher in pine plantations, while other soil characteristics were similar between vegetation types. Surprisingly, microbial biomass and density of soil mesofauna in the litter layer did not differ between vegetation types, while density and species richness of oribatid mites were higher in pine plantations. Community structure of oribatid mites differed between vegetation types with only a few species overlapping. The results indicate that quality and diversity of litter were not the major factors regulating the mesofauna community. Instead, soil animals benefited from increased habitat structure in thicker litter layers and potentially increased availability of root-derived resources. Overall, the results suggest that from a soil animal perspective, monoculture plantations are less detrimental than commonly assumed and enrichment of abandoned plantations with native tree species may help to restore tropical montane forests.

Abstract in Spanish is available with online material.

KEYWORDS
alder, degraded primary forest, Ecuadorian Andes, litter, mesofauna, monoculture, oribatid mites, pine

1 | INTRODUCTION

Montane rain forests of the high tropical Andes are among the most diverse ecosystems on earth (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000) containing exceptionally high numbers of endemic plant and animal species (Barthlott, Mutke, Rafiqpoor, Kier, & Kreft, 2005; Brehm, Strutzenberger, & Fiedler, 2013; Henderson, Churchill, & Luteyn, 1991; Myers et al., 2000). Increasingly, these ecosystems are threatened by anthropogenic disturbances, with deforestation and subsequent land-use change being among the most important threats (Ferreira, Leite, de Araújo, & Eisenhauer, 2016). Since much of the remaining primary forests in Ecuador are in protected areas (21% of all Ecuadorian forests are protected; UNEP, 2002), the main portion of recent deforestation concerns degraded primary forests, which previously have been logged in part or otherwise affected by human disturbance (Beck, Bendix, Kottke, Makeschin, & Mosandl, 2008). Large areas of degraded primary forests, especially at higher elevations, are converted into pastureland (Beck et al., 2008; Günter et al., 2009; Hofstede, Groenendijk, Coppus, Fehse, & Sevink, 2006; Tapia-Armijos, Homeier, Espinosa, Leuschner, & De La Cruz, 2015) and subsequently transformed into timber plantations, when their productivity declines (Weber, Günter, Aguirre, Stimm, & Mosandl, 2008). Currently, 90% of all forest plantations in Ecuador consist of non-native tree species, predominantly of the genera *Eucalyptus*, *Pinus*, and *Cupressus* (FAO, 2011; Weber et al., 2008). These monoculture plantations—although successful in providing local communities with timber—have led to the homogenization of the landscape (Lamb, Erskine, & Parrotta, 2005), resulting in increased susceptibility to fires and plant diseases, reduced aboveground plant and animal diversity, and changes in soil properties (Chaudhary, Burivalova, Koh, & Hellweg, 2016; D'Antonio & Meyerson, 2002; Lamb et al., 2005).

Changes in soil properties are closely linked to changes in important ecosystem functions provided by forest soils, for example, carbon storage, nutrient cycling, and erosion control. As part of the regulatory forces of ecosystem processes, the mesofauna contribute directly and indirectly to the decomposition of organic matter, nutrient cycling, and soil physical and chemical properties (Bardgett, 2002; Lavelle et al., 2006). With the plant community influencing soil characteristics, such as pH, organic carbon, and nutrient content as well as soil texture, land-use and plant community changes also impact the mesofauna community structure and their contribution to ecosystem processes (Barrios, 2007; Ekschmitt, Liu, Vetter, Fox, & Wolters, 2005; Fanin & Bertrand, 2016; Tsiafouli et al., 2015; Yesilonis, Szlavecz, Pouyat, Whigham, & Xia, 2016). Especially in a region characterized by an exceptionally high number of plant species, such as the high tropical Andes (Homeier, Dalitz, & Breckle, 2002), burning of degraded primary forest and the subsequent use as pastureland followed by a conversion into monoculture timber plantations (Günter et al., 2009) are expected to have major consequences for mesofauna communities.

The soil mesofauna community in tropical montane rain forests of the Andes is dominated by microarthropods, in particular oribatid mites, while larger macro-decomposers are rare or lacking (Illig, Langel, Norton, Scheu, & Maraun, 2005; Maraun, Sandmann, Krashevska, Norton, & Scheu, 2008). Despite their seemingly homogeneous habitat in the litter and upper soil layers, oribatid mites are exceptionally diverse and span over up to three trophic levels from primary decomposers to secondary decomposers to predators (Illig et al., 2005; Scheu, 2002; Schneider, Renker, Scheu, & Maraun, 2004; Walter & Proctor, 1998). With nearly 10,000 described species (Subias, 2018) and an estimated total of 110,000 species worldwide (Walter & Proctor, 2013), oribatid mites are the most species-rich subgroup within the Acari. They contribute not only to the breakdown of organic matter, but are also closely linked to microbial activity and biomass in soil (Barros et al., 2003; Behan-Pelletier, 1999; Dindal, 1990; Muturi et al., 2009; Nielsen, Osler, Campbell, Burslem, & van der Wal, 2012). With a lifespan of typically between one to two years and low reproductive output, oribatid mites invest strongly in defense mechanisms, such as camouflage, strong sclerotization, defensive glands, and protective structures and, as a result, are well defended and little preyed upon by mesofauna predators (Heethoff, Koerner, Norton, & Raspotnig, 2011; Heethoff & Raspotnig, 2012; Peschel, Norton, Scheu, & Maraun, 2006; Schneider & Maraun, 2009; Figure 2). Major structuring forces of oribatid mite communities, besides resource availability and quality, include soil pH and habitat space, that is, low pH and thick organic layers favor oribatid mite density and species richness (Maraun & Scheu, 2000; Ramírez Castillo et al., 2018; Schaefer & Schauermann, 1990). Changes in the availability and quality of resources are also associated with the reproductive mode in oribatid mite communities. In general, parthenogenesis is more abundant in oribatid mites than in any other group of Acari (Krantz et al., 2009). However, the percentage of parthenogenetic species and individuals varies between habitats, with harsh environmental conditions and low resource availability being associated with low frequency of parthenogenetic species (Maraun et al., 2011; Marian, Sandmann, Krashevska, Maraun, & Scheu, 2018; Scheu & Drossel, 2007). Since factors structuring the mesofauna and especially oribatid mite communities largely depend on the aboveground plant community (Eisenhauer et al., 2011; Scheu, 2001), their density, species richness, and community structure may be valuable indicators for shifts in ecosystem processes related to the conversion of degraded primary montane forest into monoculture timber plantations.

In this study, we compared the density, species richness, and community structure of litter and soil-living mesofauna, with a focus on oribatid mites, between remnants of degraded primary tropical montane rain forest (referred to as degraded forest hereafter) and monoculture plantations of native and non-native tree species.

We hypothesized that (a) the conversion of degraded forest into pastures and later into plantations results in an overall decrease in soil mesofauna density and species richness, due to reduced plant diversity, and the associated decrease in resource and niche diversity for the soil mesofauna, and (b) the density of soil mesofauna is higher in

the plantation type with thicker organic layers, that is, pine. Further, we hypothesized that (c) oribatid mite species composition is more similar between degraded forest and native alder plantations with a larger overlap in oribatid mites species compared to non-native pine plantations with more cosmopolitan oribatid mite species, and (d) the number of parthenogenetic species is higher in alder and pine plantations due to ample supply of uniform resources, that is, single-species litter.

2 | METHODS

2.1 | Study sites

The study sites were located in the Andean montane region of southern Ecuador in the valley of the regional capital Loja (Figure 1). Native vegetation in the region is upper montane forest, but the native forest has largely been replaced by pine (*Pinus patula* Schiede & Deppe), Sydney blue gum (*Eucalyptus saligna* Smith), and Andean alder (*Alnus acuminata* Kunth) plantations with some fragments of degraded primary montane forest remaining in a scattered landscape surrounding the city (Iñiguez-Armijos, Leiva, Frede, Hampel, & Breuer, 2014). In this study, we focused on pine and alder plantations

because pine is of major economic importance for timber production in the region and alder has commercial potential due to its use in other Andean countries. Alder has a rather shallow root system and forms associations with nitrogen-fixing rhizobacteria (*Actinomyces alni*; syn. *Franki alni*) as well as both ecto- and arbuscular mycorrhizal fungi (Becerra, Zak, Horton, & Micolini, 2005; Carú, Becerra, Sepúlveda, & Cabello, 2000). By contrast, pine is associated only with ectomycorrhizal fungi, but has deeper roots than alder (CAB International, 2019; World Agroforestry, 2019).

The natural upper montane forest in the Andes is characterized by an exceptionally high diversity of tree species, with up to 200 tree species per hectare in the Podocarpus National Park located in close proximity to the present study sites (Homeier, Breckle, Günter, Rollenbeck, & Leuschner, 2010). Dominant tree species in the natural forest are in the Lauraceae, Euphorbiaceae, Melastomataceae, and Rubiaceae (Homeier et al., 2002). Rooting depth is rather shallow and the mycorrhizal community is dominated by arbuscular mycorrhizal fungi (Camenzind et al., 2014; Kottke, Beck, Oberwinkler, Homeier, & Neill, 2004), with only few plant species forming associations with ectomycorrhizal fungi (Haug et al., 2004; Haug, Weiss, Homeier, Oberwinkler, & Kottke, 2005; Kottke & Haug, 2004). The degraded forest sites
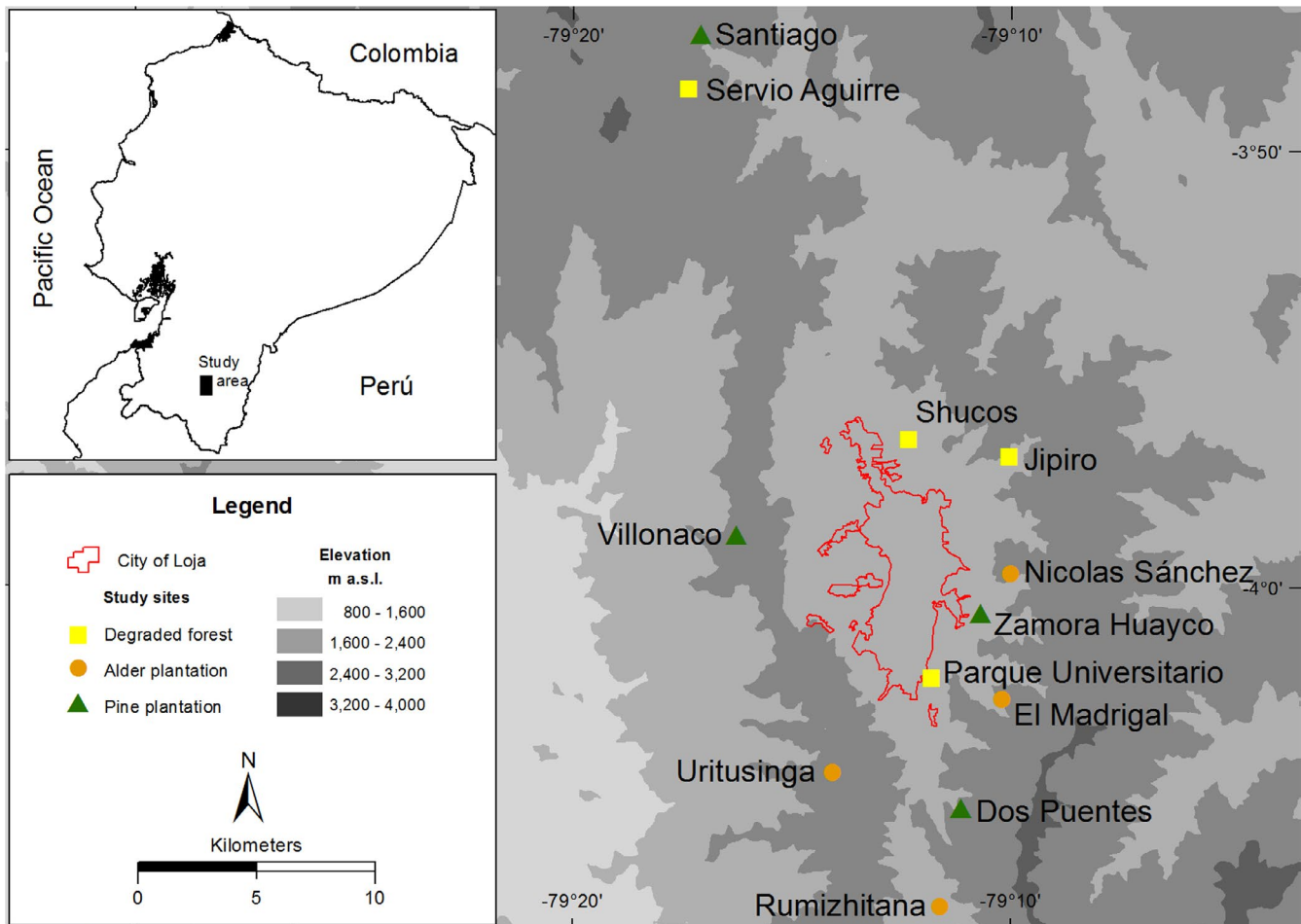

FIGURE 1 Location of the study sites comprising four replicates of degraded forests (yellow squares), Andean alder plantations (orange circles), and pine plantations (green triangles) around the city of Loja, southern Ecuador

investigated in this study are remnants of the natural upper montane rain forest in the region, which have been partially logged for profitable timber species, and typically are exposed to moderate human disturbance, such as selected logging or grazing by cattle. Tree species diversity therefore is reduced, and primary forest trees are scarce or lacking. The region has a semi-humid climate with 6–8 humid months per year; the rainy season lasts from April to July alternating with a drier season from September to March (Ortiz et al., 2006). Annual precipitation averages 947 mm/year, and mean annual air temperature is 16°C (Günter et al., 2008).

Twelve study sites were selected in the Loja valley between 2,400 and 2,600 m a.s.l.: (a) four pine and (b) four alder plantations, and (c) four degraded forests (Figure 1). All sites were located within forest fragments/plantations larger than 8 ha and on low slope areas to avoid topographic variations. Plantations were selected based on the following criteria: (a) age of trees (15–25 years); (b) similar levels of management; and (c) permission by landowner. Following common practice in the region, the plantations have not been intensively managed but left largely unattended after planting of tree seedlings, resulting in a dense understory vegetation, especially in alder plantations. In each forest fragment/plantation, one experimental plot of 24 × 24 m was established. Within each plot, four samples were taken at randomly selected points, resulting in a total of 48 sampling points for each investigated parameter; similar designs have been used to study soil characteristics and microarthropod communities in temperate regions (Klarner et al., 2014; Pollierer & Scheu, 2017). We used a soil corer 5 cm in diameter. Each core was divided into O horizon (litter layer) and Ah horizon (5 cm of mineral soil underneath the litter layer), which were analyzed separately for all parameters, including soil mesofauna abundance and diversity. Sampling was performed after at least 2 days without strong rain to ensure comparable soil moisture conditions.

2.2 | Environmental factors

Samples for habitat characteristics (pH, litter thickness, and soil water content) and litter quality (C-to-N ratio) were taken at the four sampling points within each plot. Soils in the region are dominantly Umbrisols (Quichimbo et al., 2017). For measuring carbon (C) and nitrogen (N) concentrations, an aliquot of both the litter and mineral soil was milled to powder; 3–4 mg were analyzed for C and N concentrations using an elemental analyzer (Vario EL III, Elementar) (Butenschoen et al., 2014; Marian, Sandmann, Krashevska, Maraun, & Scheu, 2017). Water content in both layers was measured from aliquots dried at 60°C for 2 days.

2.3 | Microbial parameters

At each of the four sampling points, two samples for microbial parameters were taken in close proximity (20–50 cm distance). Following the procedure established and used previously (Marian,

Brown, Sandmann, Maraun, & Scheu, 2019; Marian et al., 2017), samples were divided into litter and mineral soil layer as described above, placed in plastic bags, stored at 4°C, and transferred to Germany. Microbial basal respiration (BR) and substrate-induced respiration (SIR) were determined by measuring O_2 consumption using a computer-controlled O_2 microcompensation apparatus (Scheu, 1992). Prior to measurement, an aliquot of leaf litter was cut into pieces <0.5 cm^2 and the soil was sieved through 2-mm mesh and mixed thoroughly. Before measuring, the samples were rested for 4 days at room temperature to avoid including increased basal respiration caused by cutting of leaf litter and homogenization. Moist samples equivalent to 0.2 (litter) and 2 (soil) g dry weight were supplemented with glucose equivalent to 80 (litter) and 8 (soil) mg/g dry weight, and BR was measured for 24 h with readings taken every hour. Microbial biomass (C_{mic}) was calculated from the maximum initial respiratory response (MIRR; µl O_2 g^{-1} dry weight h^{-1}) as $C_{mic} = 38 \times$ MIRR (Anderson & Domsch, 1978; Beck et al., 1997; Joergensen & Scheu, 1999).

2.4 | Soil mesofauna

For the analysis of soil mesofauna, one additional soil core was taken at each sampling point (48 cores) and divided into leaf litter and soil as described above. Mobile soil animals were extracted by heat within 24 h after sampling (Kempson, Lloyd, & Ghelardi, 1963). Extracted animals were stored in 70% ethanol and transferred to Germany. Most animal groups were determined to order, suborder, or cohort level using Schaefer (2010) except for adult oribatid mites, which were determined to species level or sorted into morphospecies. Due to the lack of appropriate keys for determination and the high number of undescribed species, this was not possible for the families Galumnidae and Phthiracaridae, which made up 9.0% of the adult oribatid mite individuals. For the determination of the other oribatid mite taxa, the keys of Balogh and Balogh (1988, 2002) and Weigmann (2006) were used. All oribatid mite species were catalogued in the Ecotaxonomy data base (http://ecotaxonomy.org/). Species names and distribution of oribatid mites follow Subias (2018). Reproductive mode of oribatid mite species was determined according to literature (Maraun et al., 2019; Maraun, Fronczek, Marian, Sandmann, & Scheu, 2013; Marian et al., 2018) and personal communication with Dr. Roy A. Norton.

2.5 | Statistical analysis

Statistical analyses were performed using R version 3.5.1 (R Core Team, 2018) with R studio interface (RStudio Team, 2016). Differences in environmental factors (pH, litter thickness, C-to-N ratio, and water content) and microbial parameters (C_{mic} and BR) between degraded forest, and alder and pine plantations were analyzed using linear mixed-effects models as implemented in the *nlme* package (Pinheiro, Bates, DebRoy, & Sarkar, 2018). The same was done for density of

TABLE 1 Density (mean ± standard deviation, *SD*) of mesofauna groups (total mesofauna, oribatid and mesostigmatid mites, and collembolans) in the litter and soil layer in three vegetation types (alder = alder plantations, pine = pine plantations, and degraded forest = degraded primary tropical montane forests). *F* and *p* statistics given with level of significance (*$p < .05$)

| Animal group	Layer	Individuals per m^2 (mean $\pm$ SD)			Statistics	
		Pinus	*Alnus*	**Degraded forest**	$F_{2/9}$-value	*p*-value
Total mesofauna	Litter	110,612 $\pm$ 64,269	61,652 $\pm$ 37,686	84,525 $\pm$ 51,192	1.71	.2339
	Soil	17,274 $\pm$ 19,429	13,202 $\pm$ 11,852	4,835 $\pm$ 4,753	6.56	.0175*
	Total	127,886 $\pm$ 65,378	74,854 $\pm$ 37,063	89,361 $\pm$ 53,729	2.08	.1805
Oribatid mites	Litter	60,411 $\pm$ 45,206	22,650 $\pm$ 17,594	21,314 $\pm$ 14,887	3.24	.0874
	Soil	3,276 $\pm$ 4,782	922 $\pm$ 1,355	254 $\pm$ 371	2.91	.1057
	Total	63,688 $\pm$ 45,590	23,573 $\pm$ 17,23	21,568 $\pm$ 15,059	3.87	.0613
Collembolans	Litter	31,621 $\pm$ 18,617	21,823 $\pm$ 27,368	28,631 $\pm$ 27,393	1.53	.2681
	Soil	6,330 $\pm$ 7,692	2,163 $\pm$ 3,062	6,362 $\pm$ 10,497	1.56	.2616
	Total	37,984 $\pm$ 20,249	28,154 $\pm$ 29,424	30,794 $\pm$ 29,789	1.14	.3622
Mesostigmatid mites	Litter	9,130 $\pm$ 5,271	9,671 $\pm$ 11,204	19,310 $\pm$ 14,711	1.15	.3598
	Soil	2,131 $\pm$ 1,775	636 $\pm$ 881	572 $\pm$ 1,032	5.29	.0303*
	Total	11,261 $\pm$ 4,774	10,307 $\pm$ 11,116	19,882 $\pm$ 14,892	1.12	.3682
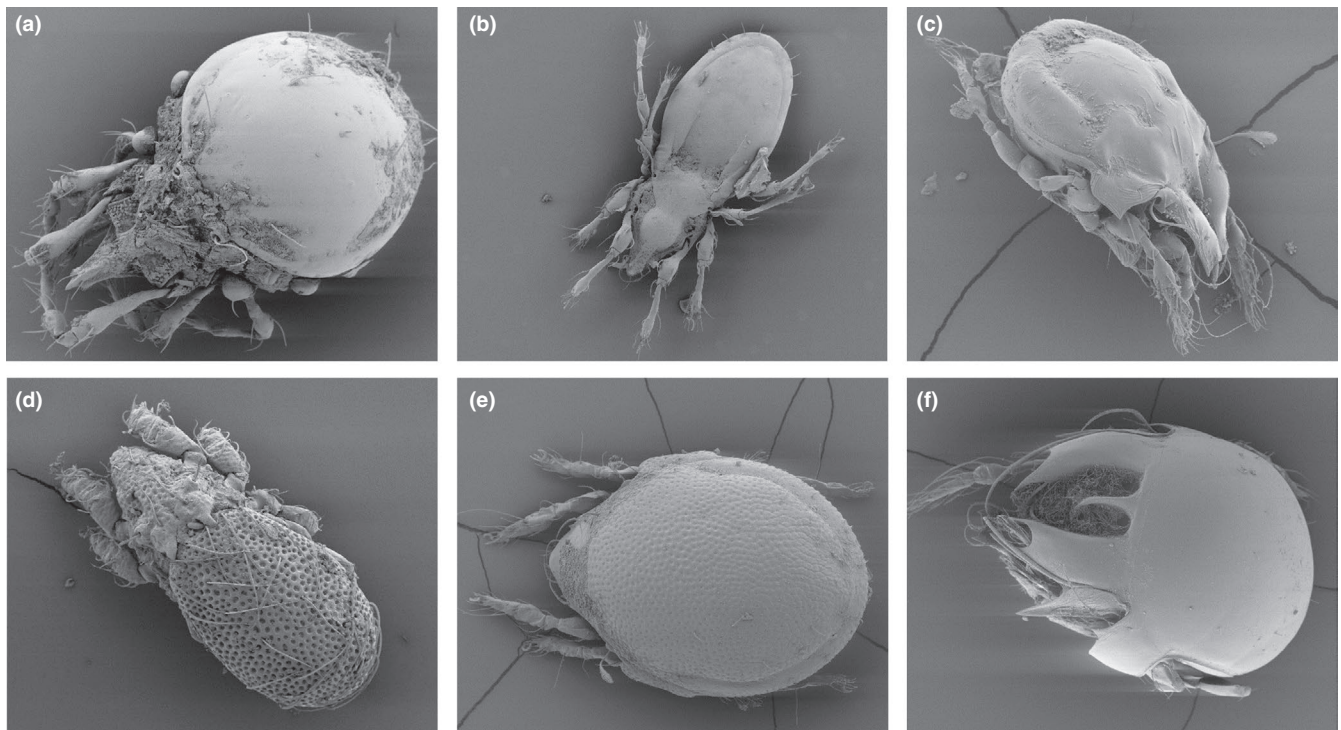
FIGURE 2 Oribatid mites from primary tropical montane rain forests of southern Ecuador sampled in the Podocarpus National Park. (a) *Rhynchoribates* cf *mirus*, (b) *Beckiella capitulum*, (c) *Cosmozetes reticulatus*, (d) *Nanhermannia elegantissima*, (e) *Rostrozetes aculeatus*, (f) *Schaleria brevisetosa*. Photograph credit: Mark Maraun and Dorothea Hause-Reitner

total soil mesofauna and dominant soil fauna groups (oribatid mites, mesostigmatid mites, and collembolans), species richness of oribatid mites, percentage of parthenogenetic individuals and taxa of oribatid mites, and the number and percentage of juvenile oribatid mites. Vegetation type (pine, alder, and degraded forest) was used as fixed factor, and sample site was included as random factor to account for replicate samples (four) taken per site. The significance of the fixed factor was inspected using the ANOVA function. Data were inspected for normality by Shapiro–Wilk test using the *mvn* package (Korkmaz, Goksuluk, & Zararsiz, 2014) prior to the analyses. Data were log-transformed except for percentage data which were arcsine-square-root transformed if necessary to improve homogeneity of variances.

Oribatid mite community composition was analyzed by discriminant function analysis (DFA) using Statistica 13.3 for Windows

(TIBCO Software Inc, 2017). Prior to DFA, dimensions were reduced to six by non-metric multidimensional scaling (NMDS) using Canoco 5.02 (ter Braak & Simlauer, 2012). Inter-relationships between environmental factors and oribatid mite species in the litter layer were analyzed using canonical correspondence analysis (CCA) as implemented in Canoco 5.02 (ter Braak & Simlauer, 2012). Environmental factors and microbial parameters in the litter layer (litter thickness, C-to-N ratio, pH, water content, BR, and C_{mic}) were included as explanatory variables; vegetation type was included as a passive variable not affecting the ordination. We considered only species present in two or more independent samples; only oribatid mites identified to species level were included.

3 | RESULTS

3.1 | Environmental factors, microbial biomass, and basal respiration

The C-to-N ratio differed between vegetation types in both litter and soil layer ($F_{2/9} = 24.33$, $p < .001$ and $F_{2/9} = 4.83$, $p = .038$, respectively). In the litter and soil layer, the C-to-N ratio was higher in pine (33.0 ± 4.7 and 17.9 ± 3.5, respectively) compared to alder plantations (17.3 ± 2.0 and 13.1 ± 1.0, respectively) and degraded forests (16.3 ± 3.9 and 11.8 ± 2.8, respectively). The water content in the litter layer showed a trend toward lower moisture content in pine plantations ($F_{2/9} = 4.12$, $p = .054$), with $29.2 \pm 6.0\%$ of total fresh weight in pine plantations compared to 41.9 ± 7.0 in alder plantations and $40.3 \pm 8.7\%$ in the degraded forests. Leaf litter thickness, water content in soil, and soil and litter pH did not differ significantly between vegetation types. Both BR and C_{mic} did not differ significantly between vegetation types in both litter and soil layers (BR: $F_{2/9} = 0.95$, $p = .423$ and $F_{2/9} = 2.40$, $p = .146$, respectively; C_{mic}: $F_{2/9} = 0.29$, $p = .753$ and $F_{2/9} = 1.09$, $p = .375$, respectively).

3.2 | Soil mesofauna

Density of total soil mesofauna in the soil layer differed between vegetation types, with the density lower in degraded forests compared to pine and alder plantations (Table 1). Total soil mesofauna density in the litter layer as well as in the litter and soil layer combined was not affected by vegetation type. Collembolan density in both litter and soil layer was not affected by vegetation type, while the density of mesostigmatid mites in the soil layer differed between vegetation types, with higher densities in pine plantations compared to alder plantations and degraded forests (Table 1). Total oribatid mite density in soil and litter layers combined tended to differ between vegetation types, with the highest density in pine plantations (Table 1). Overall, standard deviations were high in each of the mesofauna groups reflecting high spatial variation in all vegetation types.

In total, 3,162 oribatid mite individuals from 126 species were collected of which 25.1% were juvenile and not further inspected. The number of species recorded was highest in pine plantations (76) and degraded forests (76), and lower in alder plantations (52). Twenty-two of the recorded species occurred in all the three vegetation types. Pine plantations and degraded forests shared 36 species, alder plantations and degraded forests 30, and pine and alder plantations also 30. In pine plantations, degraded forests, and alder plantations, 32, 28, and 14 species were exclusive to the respective vegetation type. Overall, our dataset included 56 rare species, one recorded in only one sample. Of these rare species, 22 were recorded in pine plantations, 12 in alder plantations, and 22 in degraded forests. Overall, the majority of oribatid mite species were tropical and subtropical or had only been recorded in Ecuador, while only 15 species had a cosmopolitan distribution (Figure S1: species list in supplementary material; Figure 2: example species from tropical montane rain forest sites).

The number of oribatid mite species per soil core (henceforth referred to as species richness) tended to differ between vegetation types ($F_{2/9} = 4.2$, $p = .051$), with 15.6 ± 4.7 species per core in pine plantations compared to 8.5 ± 4.4 and 11.9 ± 4.9 species per core in alder plantations and degraded forests, respectively. Both the number and percentage of juvenile oribatid mites were not significantly affected by vegetation type. The overall percentage of parthenogenetic individuals ($41.4 \pm 8.2\%$ of total oribatid mite individuals) and species ($40.7 \pm 6.8\%$ of total oribatid mite species) was high, but both did not differ significantly between vegetation types.

Discriminant function analysis (DFA) separated the oribatid mite communities in pine plantations from those in both alder plantations ($F_{2/9} = 12.81$, $p < .0001$; squared Mahalanobis distance 10.81) and degraded forests ($F_{2/9} = 13.36$, $p < .0001$; squared Mahalanobis distance 11.28). Further, communities in alder plantations and degraded forests tended to differ ($F_{2/9} = 2.21$, $p < .062$; squared Mahalanobis distance 1.86). Canonical correspondence analysis (CCA) of the oribatid mite community separated the communities of pine plantations from the communities in alder plantations and degraded forests along both axes (Figure 3).

The test on all axes was highly significant ($p = .002$ with 499 permutations), and the axes 1 and 2 explained 7.26% and 4.01% of the total variation in the data, respectively. The explanatory variables accounted for 21.2% of the variation in the species data. High C-to-N ratio and litter thickness were associated with pine plantations, while high water content was associated with degraded forests and alder plantations. Parthenogenetic species of oribatid mites spread evenly along the first axis, but sexual species contributed more to the separation along the second axes reflecting differences between alder and pine plantations.

The most abundant oribatid mite species in the degraded forests were *Suctobelbella peracuta*, *Kokoppia* cf. *euramosa*, *Nanhermannia nana*, *Oppiella* cf. *nova*, and *Scheloribates* cf. *vulgaris* (Table 2). Dominant oribatid mite species in pine plantations were *Rostrozetes ovulum* followed by *Novosuctobelbella* cf. *andrassy*, *Ramusella* cf. *puertomontensis*, *Micropploia minus*, and *Oppiella* cf. *nova*. In alder
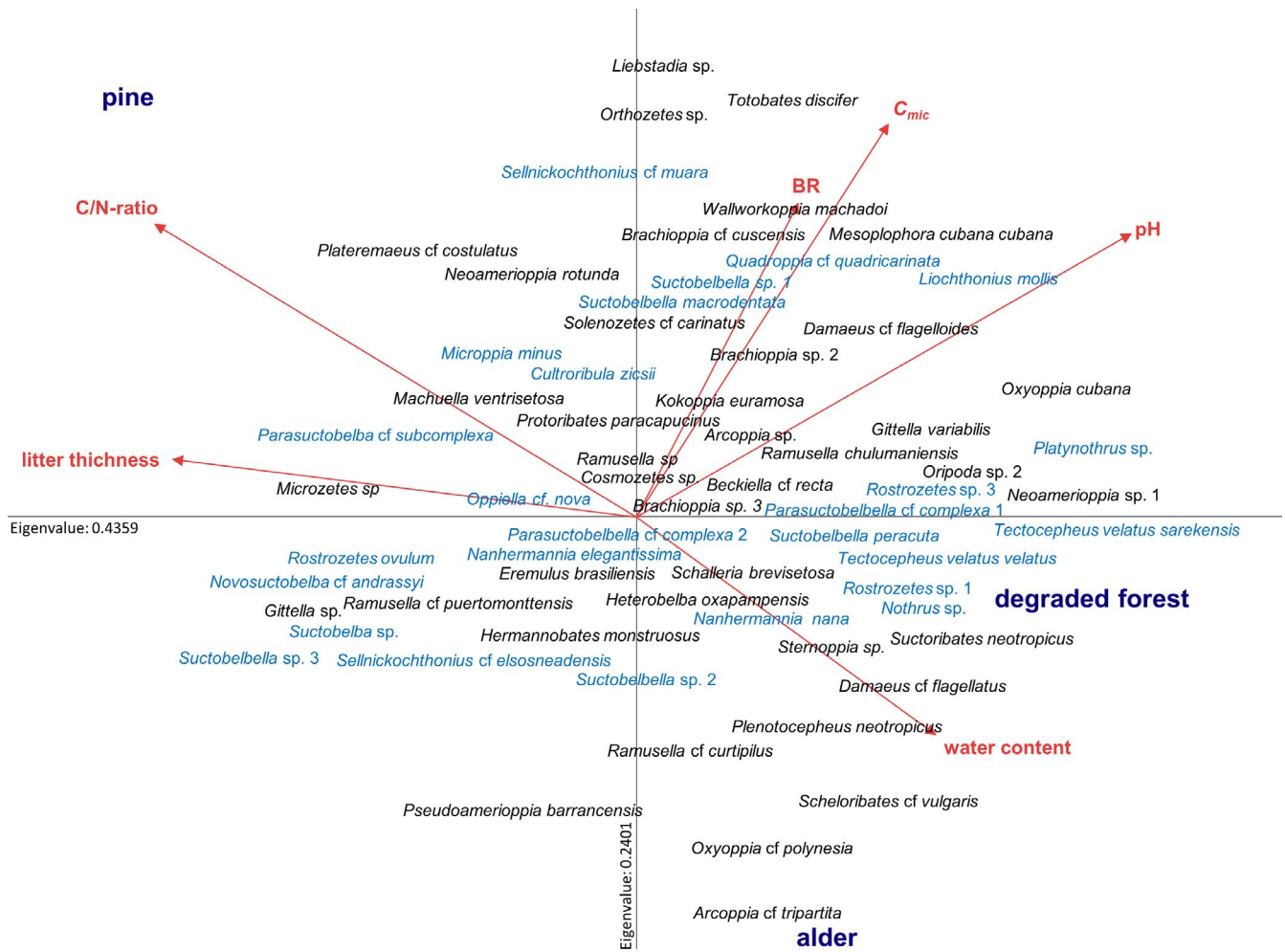
FIGURE 3 Canonical correspondence analysis (CCA) of oribatid mite species with vegetation types (alder = alder plantations, pine = pine plantations, and degraded forest = degraded primary tropical montane forests) as supplementary variables, and environmental variables in the litter layer (C/N ratio = C-to-N ratio, water content, litter thickness = thickness of litter layer, pH = litter pH), basal respiration (BR), and microbial biomass (C_{mic}) as explanatory variables. Species given in blue reproduce via parthenogenesis

plantations, *Scheloribates* cf. *vulgaris*, *Suctobelbella peracuta*, *Nanhermannia nana*, *Rostrozetes ovulum*, and *Oppiella* cf. *nova* had highest densities (Table 2).

4 | DISCUSSION

Differences in biotic and abiotic conditions between the three investigated vegetation types were not as pronounced as expected, and density of the studied mesofauna groups and species richness of oribatid mites were highest in non-native pine plantations, contradicting our first hypothesis.

Compared to natural forests, plantations harbor fewer species and often lack the appropriate conditions for the establishment of rich and abundant aboveground animal communities (Chaudhary et al., 2016; Phillips, Newbold, & Purvis, 2017). However, forest plantations can provide habitat for a number of plant and animal species, especially when compared to other anthropogenic land-use systems, such as the dominant grass and bracken fern pastures in

tropical montane regions (Barbaro, Pontcharraud, Vetillard, Guyon, & Jactel, 2005; Brockerhoff, Jactel, Parrotta, Quine, & Sayer, 2008; Carnus et al., 2006; Chaudhary et al., 2016). This is especially the case in older plantations, which often harbor a more diverse understory vegetation, pronounced organic layers, and diverse fungal and bacterial communities (Brockerhoff et al., 2008; Chaudhary et al., 2016).

In the present study, lower litter quality and water content in pine plantations, combined with the reduced diversity of litter input into the decomposer food web of monoculture plantations (Zaninovich, Fontana, & Gatti, 2016), indicate that resource quality and environmental conditions in the soil and litter layer were less favorable. These unfavorable conditions, however, did not result in reduced microbial activity, contrasting with results from a global meta-analysis (Chen, Chen, Chen, & Huang, 2019). Saprotrophic microorganisms play an important role as primary decomposers; however, the fact that their biomass distribution was not directly linked to the abundance of soil mesofauna, which differed between the three vegetation types, suggests that they are of minor importance as a

TABLE 2 Biogeographic distribution (based on Subias, 2018), density per square meter (means ± SD), and relative abundance as percentage of total oribatid mite density (% of total) for the most abundant oribatid mite species in three vegetation types (alder = alder plantations, pine = pine plantations, and degraded forest = degraded primary tropical montane forests)

Species	ind m^{-2} (mean ± SD)	% of total	Distribution
Degraded forest			
Suctobelbella peracuta Balogh & Mahunka, 1980	1,717 ± 1,345	8.06	Neotropical
Kokoppia euramosa Balogh & Mahunka, 1969	1,558 ± 2,842	7.31	Neotropical
Nanhermannia nana Nicolet 1855	763 ± 1,772	3.58	Holarctic, Neotropical, Antarctica
Oppiella cf *nova* Oudemans 1902	540 ± 908	2.54	Cosmopolitan
Scheloribates cf *vulgaris* Hammer 1961	509 ± 863	2.39	Neotropical and Oriental
Pine plantations			
Rostrozetes ovulum Berlese 1908	11,166 ± 21,133	18.48	Pantropical and subtropical
Novosuctobelba cf *andrassyi* Balogh & Mahunka, 1981	4,167 ± 8,406	6.90	Neotropical
Ramusella cf *puertomonttensis* Hammer 1962	3,499 ± 5,560	5.79	Tropical
Micrppia minus Paoli 1908	3,117 ± 4,146	5.16	Cosmopolitan
Oppiella cf *nova* Oudemans 1902	2,417 ± 2,222	4.00	Cosmopolitan
Alder plantations			
Scheloribates cf *vulgaris* Hammer 1961	3,213 ± 6,369	14.19	Neotropical and Oriental
Suctobelbella peracuta Balogh & Mahunka, 1980	1,113 ± 2,131	4.92	Neotropical
Nanhermannia nana Nicolet 1855	795 ± 1,220	3.51	Holarctic, Neotropical, and Antarctica
Rostrozetes ovulum Berlese 1908	381 ± 1,145	1.69	Pantropical and subtropical
Oppiella cf *nova* Oudemans 1902	381 ± 661	1.69	Cosmopolitan

food resource for the mesofauna community (Scheu, 2002). Instead, other biotic or abiotic factors, not assessed in the present study, for example, quality and availability of root-derived resources, availability of habitat space in the litter layer, and small-scale variations in soil type, might play a larger role in structuring the microarthropod community.

The low density of mesofauna in the soil layer of degraded forest is surprising, since that none of the measured soil environmental parameters indicate less favorable conditions in this vegetation type. From both temperate and tropical forest ecosystems, there is increasing evidence that the mesofauna community is predominantly structured by belowground characteristics of the plant community, for example, root morphology and root-derived resources (i.e., root exudates and direct feeding on roots and mycorrhizal hyphae) (Marian et al., 2019; Pollierer, Langel, Körner, Maraun, & Scheu, 2007; Schneider, Renker, & Maraun, 2005; Zieger, Eissfeller, Maraun, & Scheu, 2015). Differences in root morphology and mycorrhization between vegetation types therefore may not just reflect structural differences in the nutrient acquisition strategy and nutrient availability between the three

vegetation types, but potentially also contribute to the reduced mesofauna density in the soil layer of the degraded forests. Research into root morphology and availability of root-derived resources in the three vegetation types is necessary to evaluate their importance in structuring soil mesofauna communities in these systems.

As a note of caution, plantations may not have been established at random, but based on specific combinations of biotic and abiotic parameters related to the long-term management history of the area, such as proximity to roads, streams, and settlements. These selection criteria might have resulted in systematic differences between the studied sites and thereby affected soil characteristics and soil mesofauna community structure. However, considering the similarity of the study sites with respect to abiotic and microbial parameters, these differences likely were small.

In the litter layer, where mesofauna densities were highest, only the density of the two most abundant mite groups (mesostigmatid and oribatid mites) differed between the three vegetation types. Contrary to our hypothesis, oribatid mite density was highest in pine plantations, reaching more than three times the density in undisturbed

tropical montane rain forest in close proximity to our study sites (17,051 $\pm$ 7,486 ind./m^2; F. Marian, unpublished data). In younger (7-year-old) pine and alder plantations in the region, differences between alder and pine plantations were not as pronounced, with about 25,000 ind./m^2 in alder and 35,000 ind./m^2 in pine plantations, while in abandoned pastures, oribatid mite density was considerably lower (ca. 15,000 ind./m^2; Ramírez Castillo et al., 2018). This suggests that in particular in pine plantations, the density of oribatid mites increases as the trees mature, which is similar to patterns reported for aboveground animal groups in monoculture tree plantations such as birds (Clout & Gaze, 1984; Donald, Fuller, Evans, & Gough, 1998; Lopez & Moro, 1997) and insects (Lindenmayer & Hobbs, 2004; Pawson, Brockerhoff, Meenken, & Didham, 2008). Ramírez Castillo et al. (2018) attributed the higher density of oribatid mites in young pine plantations mainly to the thick organic litter layer in these plantations. This is consistent with the pattern in temperate coniferous forests, where thick organic layers favor high densities of soil mesofauna, due to increased habitat space (Maraun & Scheu, 2000). Although differences in litter layer thickness between vegetation types were not significant in the present study, a trend toward thicker litter layers in pine plantations was present, suggesting that oribatid mite densities might at least in part be controlled by the available habitat space.

The recorded number of species of oribatid mites in the three vegetation types (76 in pine plantations and degraded forest, and 52 in alder plantations) was similar to that in undisturbed tropical montane rain forests in the area (~80 at 2,000 m a.s.l.; Marian et al., 2018). Both pine plantations and degraded forests contain a similar number of species, suggesting that both vegetation types provide a high number of ecological niches for oribatid mites.

Mean species richness of oribatid mites per soil core resembled the patterns found for fauna density. In alder plantations and degraded forests, species richness was similar to undisturbed tropical montane rain forests in the region (7.88 $\pm$ 2.59 species per 5 cm soil core; F. Marian unpublished data). In pine plantations, however, species richness of oribatid mites was almost twice as high, suggesting that especially oribatid mites benefit from increased niche availability in pine plantations, persumably via increased litter layer thickness, changes in root morphology, and availability of root-derived resources.

Availability and structure of resources also drive the number of parthenogenetic individuals and species. According to the structured resource theory of sex, parthenogenetic reproduction dominates if resources are unstructured and in ample supply (Scheu & Drossel, 2007). In our study, the percentage of parthenogenetic species did not differ between the three vegetation types (~40%) and was similar to undisturbed tropical montane rain forests (34%; Marian et al., 2018). By contrast, in pastures and young pine plantations in the region it was much higher (75%; Ramírez Castillo et al., 2018). This indicates that resources become more scarce and structured with increasing age of plantations, thereby approaching conditions similar to those in undisturbed montane rain forests in close proximity to the study site.

In contrast to our expectation, the introduction of non-native trees did not result in a reduction of tropical oribatid mite species, with tropical and subtropical species dominating in all three vegetation types. Although species overlap was similar between the three vegetation types, the community composition of oribatid mites in pine plantations differed significantly from that in alder plantations and degraded forests. These findings indicate that, although species numbers and abundance of oribatid mites were higher in pine plantations, from a community structure perspective the native alder plantations better resemble the species composition present in degraded forest fragments, which might be due to a more diverse understory vegetation in this plantation type. However, both plantation types appear to provide suitable conditions for the establishment of functionally diverse microarthropod communities, and reforestation with both native and non-native tree species may speed up rather than retard the recovery of the decomposer food web after deforestation (Ramírez Castillo et al., 2018).

5 | CONCLUSIONS

Results of the present study did not support most of our hypotheses. Density of soil mesofauna in forest plantations was similar to that in degraded forests, while density and species richness of oribatid mites were at a maximum in plantations with non-native pine trees. Tree diversity and aboveground leaf litter quality appear not to be the major controlling forces regulating the density and community composition of soil arthropods. Beneficial conditions for mesofauna in monoculture pine plantations are presumably due to increased thickness of the organic layer in pine plantations and, potentially, differences in root-derived resource availability. Contrasting the documented decline in diversity and density of aboveground fauna with conversion of rain forest into pastures and later into plantations, our results suggest that such conversion only moderately affects the soil mesofauna. This indicates that from a soil animal perspective, monoculture plantations appear to be less detrimental than commonly assumed. Enrichment planting with native tree species in plantations therefore may accelerate the restoration of tropical montane forests and help to conserve mesofauna diversity and associated ecosystem functions.

framework of the "Knowledge transfer project—New Forests for Ecuador"(Ma 2461/9-1).

CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi. org/10.5061/dryad.dv41ns1vf (Marian et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.