Research Article

An evaluation of bess beetles (Passalidae) and their resource base in a restored Andean forest

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Abstract

Degraded lands in the Colombian Andes have been restored by means of monospecific tree plantations of native and exotic species, and by abandoning lands to natural regeneration. Both methods rapidly produce a vegetation cover that helps to stabilize soils, but the value of resulting ecosystems for wildlife needs to be evaluated. We assessed the effects of these two restoration methods on the diversity and abundance of bess beetles (Passalidae), which are important deadwood recyclers. We quantified coarse woody debris (logs and branches >10 cm diameter) and associated passalid beetle fauna in 40-year-old Andean alder (*Alnus acuminata*) plantations, adjacent natural regeneration and old-forest remnants, at 2430 m of elevation in the Central Andes. The three forest types contained the same number of logs per unit area, but wood volume was lower in alder stands than in natural forest types. Old-forest remnants contained a higher number of occupied logs and individual beetles per transect and per unit wood volume than the two other habitats. We found six species of beetle, three of which were found in the three habitats and the other three in one habitat each. Forest remnants and natural regeneration had four species each, whereas alder plantations had three species. Although beetle abundance was lower in alder stands, in the small-scale mosaic found at this site alder plantations behaved similarly to secondary forest and merged as part of the local habitat heterogeneity. Whether these results apply to larger and more isolated plantations remains to be established.

Keywords: alder, *Alnus acuminata*, Andes, Colombia, habitat restoration, xylophagous beetles.

Resumen

Las tierras degradadas en los Andes colombianos se han restaurado por medio de plantaciones monoespecíficas de árboles nativos y exóticos y por medio de regeneración natural. Ambos métodos producen rápidamente una cobertura boscosa que ayuda a estabilizar los suelos, pero el valor de estos ecosistemas para la vida silvestre debe ser evaluado. En este trabajo evaluamos los efectos de estos dos métodos de restauración sobre la diversidad y abundancia de escarabajos Passalidae, los cuales son importantes recicladores de madera muerta. Cuantificamos la madera caída (troncos y ramas de >10 cm de diámetro) y la fauna asociada de pasálidos en plantaciones de aliso (*Alder acuminata*) de 40 años de edad, bosques de regeneración natural adyacentes de la misma edad y remanentes de bosque maduro, a 2430 m de elevación en la cordillera Central. Los tres tipos de bosque tuvieron el mismo número de troncos por unidad de área, pero el volumen de madera fue más bajo en los alisales que en los bosques naturales. Los bosques maduros tuvieron un mayor número de troncos ocupados y de escarabajos por transecto y por unidad de volumen de madera que los otros dos hábitats. Encontramos seis especies de escarabajos, tres de las cuales se encontraron en los tres hábitats y las otras tres en un hábitat cada una. Tanto en los remanentes de bosque como en la regeneración natural encontramos cuatro especies, mientras que en el alisal encontramos tres especies. Aunque la abundancia de escarabajos fue más baja en los alisales, en el mosaico de pequeña escala que hay en este sitio las plantaciones de aliso se comportan de manera similar al bosque secundario y forman parte de la heterogeneidad local de hábitat. Queda por establecer si estos resultados aplican a plantaciones más grandes y aisladas.

Palabras clave: aliso, *Alnus acuminata*, Andes, Colombia, restauración de hábitat, escarabajos xilófagos.

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Introduction

Restoration of forest cover in degraded tropical lands may be accomplished by planting trees of native or exotic species or by abandoning lands to natural regeneration. The relative effectiveness of each method depends on the initial conditions of the site (e.g., state of degradation), and the availability of nearby seed sources and dispersal vectors for fleshy fruits. Planting trees, although more costly in the short term, may catalyze the rapid establishment of tree cover and speed the restoration of tropical forests and some of their ecological processes [1—4]. The long-term comparative advantages and disadvantages of these alternative restoration methods, however, are not well known, particularly regarding the effects on processes involving interactions with animals [5].

In the Colombian Andes, planting monospecific stands of native Andean alder (*Alnus acuminata*) has been a common practice to recover vegetative cover [5-7]. Alder has some characteristics that make it valuable for restoration purposes, such as nitrogen fixation and rapid growth in degraded soils [6]. However, although alder stands are rapidly invaded by native vegetation, they have lower plant species diversity when compared to adjacent forests of the same age that have regenerated naturally under the same conditions [5, 7]. They also differ in their physiognomy (absence of a subcanopy and higher canopy openness in alder stands), but are similar in some structural characteristics such as tree density and basal area distribution [5]. This paper explores whether differences in vegetation between alder plantations and secondary forest of the same age, translate into differences in the production of coarse woody debris (CWD) and the diversity and abundance of the associated bess beetle (Passalidae) fauna.

Snags and dead branches can weigh as much as 33% of the above-ground live biomass of tress with diameter at breast height (DBH) >10 cm in a tropical forest, thus containing a significant, but often overlooked, amount of stored carbon [8]. This deadwood provides an important resource for a variety of saproxylic organisms, which in turn recycle nutrients back into the system [9-12], gradually releasing about one-fourth of the carbon into the soil [13]. Therefore, wood decomposer organisms strongly influence productivity of the forest [14-16]. The fauna associated with this process is surprisingly rich. As many as 56% of beetle species in several temperate forests are saproxylic [10]. However, saproxylic insects are highly vulnerable to management schemes that affect the availability and characteristics of decomposing wood [10, 11, 17].

Bess beetles are an important component of the wood decomposing macrofauna of tropical forests (Fig. 1). Bess beetles are subsocial insects that colonize partly decayed wood, where they build galleries and nest [18]. Adults spend their life span inside a trunk and exhibit parental care of larvae. Adults feed wood containing traces of excrements to the larvae, which pass on gut microorganisms. Adults may produce several broods in the same gallery system [18]. Wood decomposition by bess beetles may be a significant part of total wood recycling in forest ecosystems [19]. For example, depending on the size of the beetle, these insects may recycle up to 29% of the wood of *Liquidambar styraciflua* [20]. Rates of wood decomposition depend on factors such as the species of wood, secondary compounds, state of decay, environmental conditions around the fallen log, and species and size of beetle.

At Ucumarí Natural Regional Park, in the central range of the Andes of Colombia, monospecific stands of Andean alder were planted over 40 years ago to promote the recovery of forest cover in pastures. Patches of pasture adjacent to alder stands were allowed to regenerate naturally, resulting in a continuous mosaic of patches of same-age alder-dominated and mixed-canopy forest (Figure 1). Six or more species of bess beetle may be found in sympatry in these high-elevation montane forests of the northern Andes [21].

We conducted this study to ascertain whether, after 40 years, the community of bess beetles had been restored in these forests, and if bess beetle diversity and abundance differed between alder plantations and secondary forest, in particular because of the monodominance and size homogeneity of alder in plantations [5]. We compared the bess beetle fauna of alder and second-growth forest of the same age, with that of old-growth forest remnants, and measured the resource base of fallen logs and branches, as a possible factor determining differences in beetle faunas among habitats.

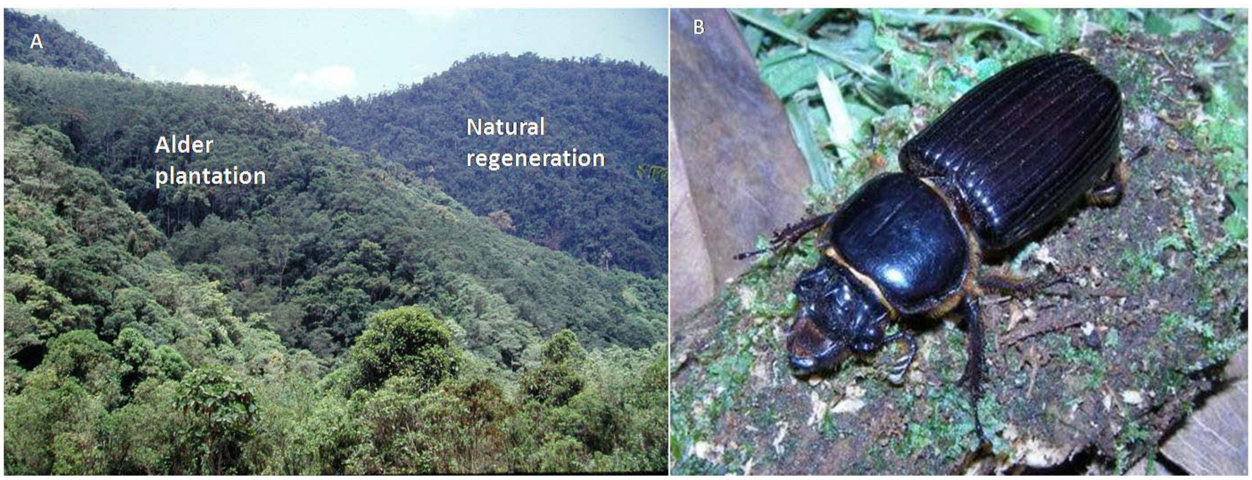

Fig. 1. A. **Mosaic of alder plantations and natural regeneration at Ucumarí Natural Regional Park in the Central Andes of Colombia. Note the homogeneous canopy of the alder stand. B. *Veturius aff. transversus,* a passalid beetle found at Ucumarí.**

Methods

Study area

Ucumarí Natural Regional Park is a 4,240 ha protected area located on the western slope of the Central Cordillera of the Andes of Colombia, east of the city of Pereira, Risaralda Department (Fig. 2). Ucumarí protects the Otún River drainage between elevations of 1,750 and 2,600 m. Average annual rainfall is around 2,600 mm, distributed bimodally with peaks of precipitation in April and October. Before protection programs began, most of the land flanking the river was used for cattle ranching. Old-growth forest remained only on the steepest slopes and in narrow strips on the valley bottom, along the river. In the 1960s the local government started restoring forest cover for soil stabilization and erosion control, to secure a constant and clean supply of water for a growing urban and rural population [22]. At the upper elevations, 2,400 to 2,600 m, monospecific stands of alder and other tree species were planted throughout the landscape. These stands were not managed and are presently overgrown with native vegetation, although the canopy is monodominant. As a result of this restoration program, 4 to 10 ha patches of alder-dominated and naturally regenerated and old-growth mixed forest lie intermingled on the foothills and valley bottom, in an area of 66 ha.

Fig. 2. Location of the study area on the western slope of the Central Andes of Colombia, east of Pereira.

Between August 1996 and January 1997, we sampled four 50 x 2 m transects in different patches of each forest type. Sampling areas were separated by at least 100 m. We sampled bess beetles in all fallen logs and branches (minimum diameter 10 cm) or portions that fell within the transect. All logs were measured and broken into pieces with a small ax. All beetles found under the bark or in internal galleries were collected. Because sampling was destructive of both the resource base and the beetles and we were working in a protected area, we opted to keep sample size small to minimize impact. A research and collecting permit in the park was granted by the Corporación Autónoma Regional de Risaralda. Beetle voucher specimens were deposited at the collections of the Humboldt Institute, Bogotá, Colombia, and Instituto de Ecología Tropical, Xalapa, Mexico.

We assigned each log to a decay category as follows: 1) bark intact and wood hard, no invading roots; 2) bark intact but soft, sapwood soft, heartwood hard, roots invading the sapwood; 3) bark partially or completely missing, sapwood missing or very soft, heartwood hard, roots reaching the core; and 4) bark missing completely, all wood soft and easy to penetrate, completely invaded by roots [23]. All four decay categories were used to test for differences in decay level of logs. However, because bess beetles rarely used logs with little decay (category 1), we excluded this category to report the number of usable logs.

We analyzed data with Kruskal-Wallis non-parametric ANOVA. To test for spatial autocorrelation in the number of beetles per log in transects, we obtained a semivariogram for each transect. All transects produced flat lines, indicating no spatial dependence [24]. Therefore, for log-related variables we treated logs as independent sampling units.

Table 1. Mean values (±SD, sample size in parenthesis) of woody debris resource base in three habitat types at Ucumarí Regional Park, 2430 m in the Central Andes of Colombia.

Variable	Alder stands	Secondary growth	Old forest	Test[a]	df	P
Number of logs	10.5±2.9 (4)	12.5±1.3 (4)	13.0±2.9 (4)	1.65	2	0.43
Number of usable logs	8.8±3.6 (4)	12.3±1.7 (4)	12.5±3.1 (4)	2.65	2	0.26
Decay level	2.9±1.1 (42)	2.8±0.8 (50)	2.9±0.9 (52)	0.33	2	0.84
Basal area (m^2/ha)	10.7±2.03 (4)	22.15±7.93 (4)	20.31±4.50 (4)	5.69	2	0.06
Wood volume (m^3/ha)	2.40±0.20 (4)	5.91±2.67 (4)	5.96±1.67 (4)	7.54	2	0.02
Log diameter (cm)	10.5±4.5 (42)	12.9±7.7 (50)	13.1±5.3 (52)	5.76	2	0.05
Log length (m)	2.2±1.2 (42)	2.7±1.9 (50)	2.8±1.6 (52)	1.01	2	0.60
Log surface (m^2)	0.7±0.5 (42)	1.1±1.1 (50)	1.2±0.9 (52)	7.06	2	0.03

[a] Kruskal-Wallis nonparametric ANOVA.

Results

The three habitat types, i. e., old-growth forest remnant, 40-year-old secondary forest and 40-year-old alder-dominated forest, did not differ in total number of fallen logs per plot, or in number of usable logs (excluding decay level 1; Table 1). The habitats did differ, however, in the total wood volume available. Forest remnants and natural regeneration had three times the wood volume as alder stands (Table 1). This difference was due to logs being thinner in alder forest than in the two other habitats. There was a marginally significant difference in basal area of CWD, which was twice as much in the natural regeneration and the mature forest as in the plantations (Table 1). There were no differences in log length among habitats (Table 1). Because logs were thinner in the alder habitat, their surface area was also smaller (Table 1). There were no differences in log decay level among habitats (Table 1).

We found six species of bess beetle in the 12 plots (Table 2). Three species were found in the three habitat types and the other three were found in only one habitat each. Forty-eight (36%) of the 133 sampled logs had at least one beetle, but their distribution was uneven across the three forest types.

Old-forest remnants contained the highest number of occupied logs, while alder plantations contained the least (Table 3). Occupied logs contained between 1 and 15 adult beetles belonging to 1 to 3 species. Old-forest remnants had about three times the number of beetles per transect as the two other forest types (Table 3). The number of beetles per unit volume of wood sampled was also significantly higher in old-growth forest (Table 3). Most individual beetles (59%) belonged to a single species (*P. irregularis*). Because of its numeric dominance, differences in abundance of this species determined the differences observed among forest types in number of individual beetles.

Table 2. Total number of adult individuals of six species of bess beetle in three habitat types at Ucumarí Regional Park.

Species	**Alder stands**	**Secondary growth**	**Old forest**
Passalus irregularis (Kuwert 1891)	25	24	99
Passalus rex (Kuwert 1989)	0	14	0
Passalus confusus (Kuwert 1891)	3	4	6
Passalus zangi Hincks 1934	8	6	14
Veturius aff. transversus (Dalman 1817)	0	0	2
Unidentified	0	0	1
Total	**36**	**48**	**122**

Discussion

The three forest types had an equivalent number of logs per unit area, with the same degree of decay. However, alder plantations and secondary growth of the same age differ in live and snag basal area [5], and the amount of CWD generated. This result is similar to that reported for another tropical site (La Selva, Costa Rica), where CWD does not correlate with measures of the stand's structure but correlates with the stand's dynamics as measured by the number of standing dead trees [8]. Although having the same live basal area [5], plantations generated only one-third the volume of CWD as the 40-year-old natural regeneration. This was because logs in the alder-dominated forest were thinner. This coincides with a similar pattern observed in snag structure in adjacent permanent vegetation plots; standing dead trees in the plantations are equivalent in abundance, but significantly thinner than those found in the natural regeneration (C. Murcia, unpubl. data). Snag basal area in the plantation was two-thirds the basal area in the natural regeneration [5]. In this study, the secondary forests are shedding a significantly higher amount of CDW than expected from the stands' basal area (an average of 75% of the equivalent of the stands' basal area is represented in fallen logs, compared to an average of 35% for the plantations). We observed no obvious signs that would indicate that this is the result of disease or catastrophic disturbance for the secondary forests. Both natural regeneration and the plantations have continued to accrue basal area several years after this study was conducted (Murcia, unpubl data), indicating that the rates of CWD observed are not the result of a decaying forest.

The two mixed forests had volumes of CWD two to three times higher than those reported for mature tropical lowland rainforests in Benin [25] and Queensland, Australia [26], and for undisturbed dry forests in southern Mexico [27], in spite of having equal or lower live basal areas, but 50-100% lower than those reported for Costa Rica [8] and eastern Brazilian Amazon [28]. This suggests a more dynamic nature of the CWD in this high-elevation forest compared to some lower-elevation tropical forests.

Differences in resource base between the three habitats may be caused by two factors: stand age and initial conditions. The alder plantation and the secondary forest, both of which are about 40 years old, are still accumulating biomass, and less than 5% of the individuals have a DBH equal or larger than 30 cm (Murcia, unpubl. data). Therefore, mean trunk size is smaller in these forests than in the mature forest. Alder plantations and secondary forests are the same age, but in the former all canopy trees belong to the same species and were planted at even distances, thus reducing the variance in growth and biomass accumulation rates. In consequence, biomass is evenly distributed among trees, with a lower mean diameter. In non-planted forests, in contrast, there is higher heterogeneity in distances between trees, which would allow for a few relatively isolated individuals to accrue wood at a faster rate than those that grew more clumped.

Table 3. Mean values (±SD, sample size in parenthesis) of abundance and species richness of bess beetle in three habitat types at Ucumarí Regional Park, 2430 m in the Central Andes of Colombia.

Variable	**Alder stands**	**Secondary growth**	**Old forest**	**Test[a]**	**df**	**P**
No. of occupied logs/transect	2.5±1.3 (4)	3.8±1.0 (4)	6.0±1.4 (4)	6.83	2	0.03
Number of beetles/transect	9.0±6.7 (4)	12.0±5.4 (4)	30.5±11.1 (4)	7.73	2	0.02
Number of beetles/m^3 wood	40.0±105.7 (42)	33.9±65.4 (50)	81.7±152.8 (52)	5.79	2	0.05
Number of species/transect	2.25±0.5 (4)	2.50±0.6 (4)	2.75±1.0 (4)	0.84	2	0.60

[a] Kruskal-Wallis nonparametric ANOVA

High volumes of CWD did not translate into high species diversity of bess beetles. This site is located in the upper limit of distribution of many insect groups; thus insect diversity is expected to be low. Differences in CWD between the plantations and the mixed forests did not translate into a difference in the number of beetle species per plot either, but with only six species, three of which were rare, this comparison is not biologically significant. However, beetles were more abundant in old-growth forest than in the two other habitat types.

One species (*P. irregularis*) was very abundant and drove the differences among habitats in number of individual beetles. This is a species with a wide geographic distribution (P. Reyes-Castillo and G. Amat-García, pers. comm.), so presumably it has plasticity in habitat and resource use. This is an underbark species, i. e., it feeds and nests just under the bark. Because logs in old-forest remnants had a larger diameter than in other forest types, the surface area of bark is larger in this habitat. This may explain the abundance of this species in mature forest.

Habitat patches in our study area are intermixed in the landscape, and beetles are capable of flying. Therefore, they are expected to be able to colonize all habitats. Species that depend on patchy resources would be expected to respond more strongly to the distribution of resources than to habitat characteristics such as vegetation structure and composition. The diversity of passalid beetle species does not seem to be influenced by tree diversity, and a study in Mexico found no differences in passalid communities between primary and secondary forests [29]. Our study, however, revealed lower numbers of beetles per cubic meter of wood in the monodominant plantation and the secondary forest than in mature forest. In other tropical forests, saproxylic beetles responded to the characteristics of the forest structure [30, 31]. Here, we found that bess beetles' abundance did not respond to the higher availability of wood in the natural regeneration, both as CWD and as standing snags. It is unclear whether this is because 40 years may not be sufficient to accrue a full complement of species and population densities, or whether the quality of the wood is substandard from the beetles' perspective.

Implications for conservation

In contrast to other insect groups such as leaf-litter arthropods and dung beetles that have recovered well at this site [32, 33], restoration of bess beetles and other wood decomposing fauna is a process that requires many decades [10], as the presence of large fallen logs depends on forest age. Clearly 40 years is not sufficient to restore a full community of bess beetles in these forests. However, because alder is a fast-growing species, it rapidly produces woody debris that provides some habitat for saproxylic organisms. Although beetle abundances in alder stands are reduced compared to mature forest, they are similar to secondary forest of the same age. Whether alder plantations are an adequate restoration tool depends on the landscape context. Alder seems to be providing habitat for bess beetles in our study area, because of the small-scale patchiness and because sources of colonization were available nearby. It remains to be seen whether these results apply in larger and more isolated alder plantations.

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