

Diversity and community structure of geometrid moths of disturbed habitat in a montane area in the Ecuadorian Andes

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Abstract: The diversity and faunal composition of geometrid moths (Lepidoptera: Geometridae) was investigated at two sites within an anthropogenically disturbed habitat mosaic at 1950 m and 2005 m a.s.l., in the vicinity of intact Andean montane rainforest in southern Ecuador. A total of 629 specimens belonging to 197 species were collected. The results were compared with those from ten sites of undisturbed forest habitats within an elevational range of 1800–2212 m. The local diversity of the moths at disturbed sites was surprisingly high (Fisher's alpha: 86.1 and 86.8; rarefied species number at the level of 250 specimens: 117 and 113; extrapolated species number, estimator Chao 1: 220 and 303). Forest successions and remnants probably serve as habitats for many species, but diversity is possibly overestimated due to the presence of 'tourist species' from adjacent forests. Disturbed habitats were characterized by a low diversity in the genera *Eois*, *Bonatea* and *Herbita*, probably due to the absence of their potential host plants (e.g. *Piper* species). Only three moth species represented by more than three individuals were found exclusively in disturbed habitats (*Eupithecia densicauda*, *Pero obtusaria*, '*Sabulodes muscistrigata*'). Some 25 species profited from disturbance, among these were six species of the genus *Eupithecia*. The proportion of species present with only one specimen was high (56 and 62%), and species dominance was low (Berger-Parker index: 7.9 and 5.8%). In two-dimensional scaling based on the CNESS index of dissimilarity, disturbed sites are separated from the forest sites. The conservation of secondary forest remnants and natural forest appears to be essential for the survival of the very species-rich Andean geometrid moth communities.

Key words: Andes, disturbance, Ecuador, Geometridae, herbivorous insects, moths, Lepidoptera, rainforest

INTRODUCTION

Most tropical rainforests are characterized by their stunning biological diversity. A major proportion of this diversity is formed by insects, the animal group comprising the largest species number on earth. The Andean rainforests are acknowledged to be diversity hotspots on the planet for endemic vascular plants and vertebrate species (Myers et al. 2000). Insect groups such as butterflies are very species rich in the Western Amazon basin and in the Andean foothill region (Robbins & Opler 1997). However, there are surprisingly few studies on insect diversity within the mountain

regions of the Andes (e.g. Janzen et al. 1976, Braun 2002, Brehm 2002, Süßenbach 2003).

Worldwide, pristine habitats are being lost at an alarming rate, and even the remotest areas of the Amazonian rainforest face fragmentation and degradation within the coming decades (Laurance 1998). Most Andean rainforests have already been destroyed and the remnant habitat islands are threatened by fire and logging, and by transformation into pasture or plantations of exotic tree species. The impact of these different land use practices on species-rich insect communities native to the rainforest is largely unknown.

Many studies on the impact of disturbance and management practices have used butterflies as models as these are probably the best known large insect group (e.g. Willott et al. 2000, Hill et al. 2001, Lewis 2001, Stork

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et al. 2003). However, butterflies form only one charismatic fraction of insect diversity, and the responses of this group to habitat alteration might not reflect those of other taxa such as moths (Ricketts et al. 2002). Geometrid moths have been chosen as model group in a number of environmental studies in tropical regions, mainly in South East Asia and Australia (Holloway et al. 1992, Chey et al. 1997, Intachat et al. 1997, 1999, Kitching et al. 2000, Schulze 2000, Beck et al. 2002), but also recently in South America (Brehm 2002), and in Africa (Axmacher et al. 2004). With more than 21,000 described species, Geometridae are one of the three most species-rich moth families. Their taxonomy is relatively advanced (Scoble 1999), and the adults can easily be attracted with blacklight tubes. They have been described as a suitable group in which to study the effects of forestry practices because of their weak flight ability and the high habitat fidelity (Thomas 2002).

Available data suggest that geometrid moths are sensitive to habitat alterations. For example, Kitching et al. (2000) showed that the proportion of geometrid moths among Macrolepidoptera decreased with increasing levels of disturbance in Australia. Holloway et al. (1992) detected a considerable loss of lepidopteran diversity due to logging activities in Borneo, and showed that major groups within the Geometridae belonged to the most vulnerable taxa. A loss of geometrid diversity due to anthropogenic disturbance was also confirmed by Beck et al. (2002) in Borneo. Agricultural areas and young secondary forest had a significantly lower diversity compared with old growth forest.

Few studies have investigated the effects of disturbance on moth communities in the Neotropical region. One of the rare exceptions is that by Ricketts et al. (2001) which found a decreased proportion of geometrid moths in agricultural habitats in Costa Rica. Therefore, we began to investigate the effects of disturbance on geometrid moth diversity in the vicinity of an intact Andean montane rainforest. The aim of this paper is to provide the first quantitative species-level data set from two anthropogenically disturbed sites in this region, and to compare the results with data from ten adjacent forest sites (Brehm 2002, Brehm et al. 2003b). We wanted to test the hypothesis that disturbed habitats have a significantly lower geometrid moth diversity than forest habitats. We expected to find a decline in hostplant specialists

such as members of the genus *Eois* as well as connected shifts in faunal composition. We also assumed that ensembles from the disturbed sites would be separated in ordinations, and that fewer species would reach high relative abundances.

METHODS

Study sites

The study area in southern Ecuador is situated within the Eastern Cordillera of the Andes and belongs to the province of Zamora-Chinchipe. It lies at the northern border of the Podocarpus National Park, which comprises 146,280 ha of mostly undisturbed vegetation at elevations ranging from 1000 to 3600 m above sea level (Madsen & Øllgaard 1994). Two sites in disturbed habitats were investigated for this study. The geographical locations of the plots were 3°58.37' S, 79°4.88' W, 1950 m a.s.l. (D1), and 3°58.13' S, 79°4.68' W, 2005 m a.s.l. (D2). Altitude and geographical coordinates were measured using a Garmin GPS III instrument. Both study sites were situated in a landscape mosaic with a variety of land-use types including cattle pastures, bracken fallow, plantations of introduced *Pinus patula*, low-growth secondary forest and large landslide areas induced by road-building. Moth diversity within these disturbed habitats was compared with undisturbed or slightly disturbed forest sites nearby within the same elevational range. An aerial photograph of the study area shows the position of the study sites (Fig. 1).

Results on alpha- and beta diversity as well as on faunal composition of these sites were provided by Brehm (2002), Brehm & Fiedler (2003), and Brehm et al. (2003a, b). From these studies, sites 3a & b, 4a & b, 5a & b, 6a & b and 7a, & b, situated between 1800 and 2212 m a.s.l., were selected for comparison. Geographical information was provided by Brehm (2002) and Brehm & Fiedler (2003). Annual precipitation reached around 2000 mm without a marked dry season, and the average monthly temperature was 15.6°C, as measured at a local climate station at an altitude of 1952 m a.s.l. (P. Emck, personal communication).

Sampling and identification of moths

Moths were sampled manually using portable

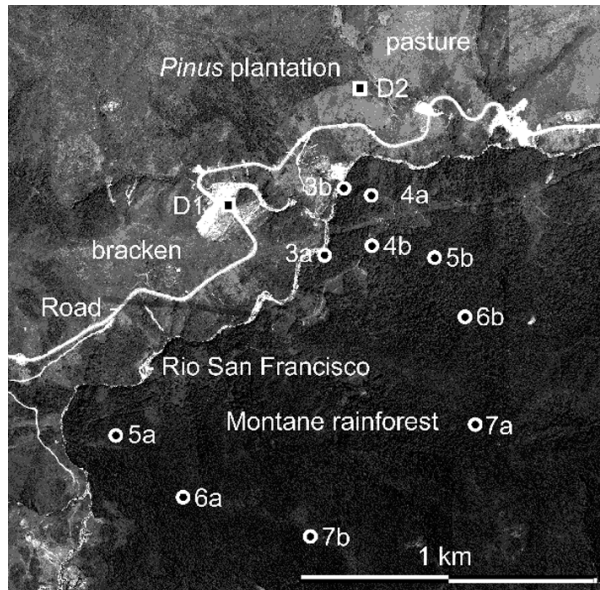


Fig. 1. Aerial photograph of the study area in southern Ecuador, dated from November 2000. Sites 3a (1800 m) to 7b (2212 m) are situated in undisturbed or slightly disturbed montane rainforest at the southern slope of the Rio San Francisco. Sites D1 and D2 are situated in a mosaic of disturbed habitats at the northern slope of the Rio San Francisco. This includes a paved road, large anthropogenically induced landslides, pastures, abandoned farmland with bracken and shrubs, plantations of exotic *Pinus patula*, and secondary forest remnants. Note that the figure is composed of several photographs. Original photographs courtesy of E. Jordan.

light-traps consisting of two 15 W actinic tubes (Sylvania blacklight-blue, F 15 W / BLB-TB and Phillips TLD 15 W 05) and a white gauze cylinder (height 1.60 m, diameter 0.60 m). Sampling methods were described and discussed by Brehm (2002). Light-traps were run during the peak of moth activity at dusk between 18.30 and 21.30 local time. Site D1 was sampled on 17th October and 26th November 2000, and site D2 was sampled on 16th October and 26th November 2000. The number of samples was low, but samples themselves were large, and a meaningful analysis appeared to be appropriate. Forest sites were sampled three to four times in April, May, and December 1999 (Brehm 2002, Brehm & Fiedler 2003). Seasonal effects with regard to changes in moth diversity and species composition in the study area are expected to be of little overall influence (Brehm 2002, Süßenbach 2003).

The moths were identified in the Natural History Museum in London (BMNH), the National Museum of Natural History in Washington D.C. (USNM), the American Museum of Natural History in New York

(AMNH) and the Zoologische Staatssammlung München (ZSM). Of 197 morphospecies collected at the disturbed sites, a noticeably high number of 139 (71%) could be identified provisionally at species level. The remainder were determined to genus. Nomenclature follows Pitkin (2002) for the largest subfamily Ennominae and otherwise follows Scoble (1999). A list of all species sampled at the disturbed sites is provided in Appendix 1.

Statistical analyses of diversity

The choice of appropriate measures of alpha diversity for geometrid moth assemblages from the study area was discussed by Brehm et al. (2003b). In accordance with this study, and in order to ensure the reliability of the results, three different measures were applied here to determine local diversity of the sites: Fisher's alpha of the log-series, rarefied species number, and extrapolated species number (Chao 1 estimator).

Fisher's alpha (Fisher et al. 1943) is mainly influenced by the frequency of species of medium abundance and has been proven to be sample-size independent and a reliable measure of diversity (Kempton & Taylor 1974, Hayek & Buzas 1997). The fit of the log-series distribution was tested using a program by Henderson & Seaby (2001). While the ensemble in site D1 fits the log-series distributions, that of site D2 does not ($p < 0.005$, 'too many' rare species). However, Fisher's alpha was used because of its proven robustness even if the distributions of relative abundance differ from a log-series (Wolda 1983). Diversity differences between disturbed sites and forest sites were tested for significance with the Solow test implemented in Henderson & Seaby's (2001) program. Rarefied species numbers are particularly useful in samples of different size (Hurlbert 1971). Here, rarefied species numbers at the level of 250 specimens were calculated using a program developed by Kenney & Krebs (2000). The abundance-based estimator 'Chao 1' was applied in a number of studies (e.g. Thomas 1996, Beck et al. 2002, Axmacher et al. 2004). Analyses were performed using the program EstimateS 6.0b1 (Colwell 2000) with the bias-corrected formula.

Faunal composition was measured using the proportions of species numbers of taxa within Geometridae and the two largest subfamilies, Ennominae and Larentiinae. Analysis of faunal

composition is a common method used for comparing the proportions of families of Macrolepidoptera (e.g. Holloway et al. 1992, Chey 2000, Kitching et al. 2000, Ricketts et al. 2001), but still rarely used at the family- or subfamily-level (but see Holloway 1987, Brehm & Fiedler 2003). Geometridae were analyzed at the level of the four subfamilies Ennominae, Larentiinae, Geometrinae and Sterrhinae. Within Ennominae, tribal composition was analyzed, including the tribes Azelinini, Boarmiini, Caberini, *Cratoptera* group, Macariini, Nacophorini, Nephodiini, Ourapterygini, Palyadini, and genera not assigned to tribe. Within Larentiinae, the three largest genera *Eois*, *Eupithecia* and *Psaliodes* as well as the remaining genera were analyzed, since a reliable tribal classification of Neotropical Larentiinae is not currently available.

The two samples from disturbed habitats and the ten samples from forest sites were ordinated using non-metric multidimensional scaling (NMDS). This,

in combination with the NESS or CNESS index of (dis-) similarity, was recommended as an analytical tool by Brehm & Fiedler (2004). The CNESS index was calculated (Trueblood et al. 1994) using the computer program COMPAH (Gallagher 1999). We chose an intermediate value of sample size parameter m of CNESS because the stress value of two-dimensional scaling was the lowest (0.05). The CNESS matrix with m set to 36 showed the best correlation with Kendall's tau with CNESS $m = 1$ and $m_{\max} = 264$. This optimum of m was determined using a Matlab code written by E. Gallagher (personal communication). Ordinations based on other indices of (dis-) similarity such as Sørensen's index, and Grassle and Smith's (1976) NESS index with different m , as well as correspondence analysis yielded very similar results and are therefore not shown. All standard statistical analyses were performed with the program Statistica 5.5 (StatSoft, Tulsa, UK).

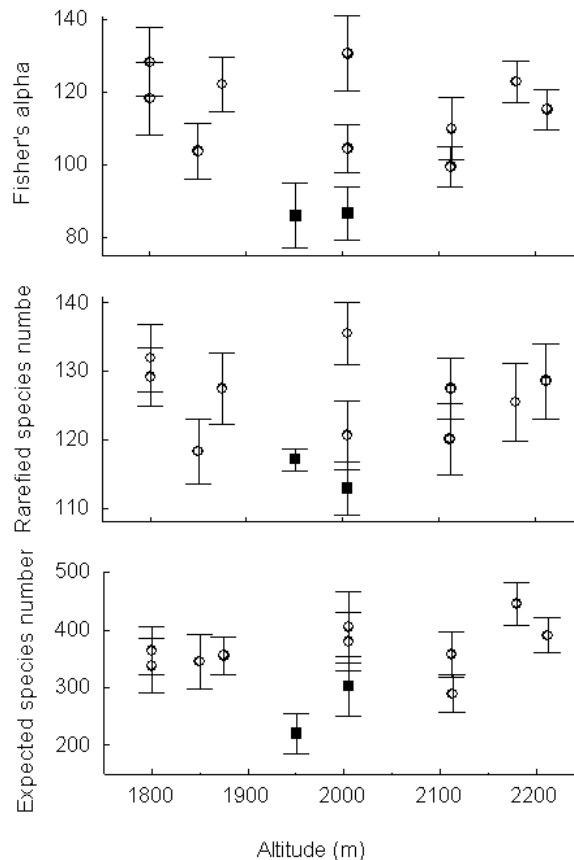


Fig. 2. Alpha diversity of geometrid moths at disturbed sites (two filled squares) compared with undisturbed forest sites (ten open circles) in a montane region in southern Ecuador, using three measures of diversity. Rarefied species number was calculated for a shared number of 250 specimens, and expected species numbers are based on the calculation with the estimator Chao 1. Error bars indicate ± 1 SD.

RESULTS

Alpha diversity

Figure 2 shows geometrid diversity at the two disturbed sites compared with the forest sites. Independent of the measure applied, disturbed sites show a lower diversity than nearly all forest sites. However, the diversity of the disturbed habitats still achieves a very high absolute level, and the difference from many of the forest sites is smaller than it was expected. The results are not fully consistent between the three measures applied.

Fisher's alpha reaches high values of 86.1 and 86.8 for site D1 and D2, respectively, and shows a clear separation between the disturbed sites and the forest sites (Figure 2). However, only eight of the 20 pairwise comparisons are significant according to the Solow test. Forest sites 3a and 5b are significantly more diverse than D1, and forest sites 3a, 3b, 4b, 5b, 7a and 7b are more diverse than D2.

The rarefied species number at the level of 250 specimens is lower at both disturbed sites (117 and 113 respectively) compared with all forest sites. However, these values have a magnitude similar to

those of sites 4a, 5a, and 6a (118, 121, 120 species respectively), and, based on overlapping 95% confidence intervals (which can be estimated as expected species number $\pm 1.96 \times SD$), these differences are not significant.

The extrapolated species number of site D1 is lower (220) than for all forest sites, but the extrapolated species number of site D2 (303) reaches the same magnitude as a number of the forest sites and is even higher than the estimate of site 6b.

Both disturbed sites have a very high proportion of species that were sampled with only one individual (D1: 56%, D2: 62%). Forest sites have a median of 53% singletons with a range between 41% (site 7a) and 63% (site 3a).

Ensemble structure

The faunal composition of geometrid moth ensembles of the disturbed sites shows no fundamental differences from that of the forest sites. Nevertheless, there are some considerable effects with regard to proportional changes and the representation of certain taxa. Table 1 provides

Table 1. Differences in faunal composition (proportions of species and individuals) of disturbed habitats (two sites) compared with undisturbed forest habitats (ten sites). The values of disturbed habitats that do not fall within the range of proportions observed at the forest sites are printed in bold. min – max: minimum and maximum values of forest sites.

	Species		Forest		Individuals		Forest	
	Disturbed D1	D2	median	min – max	Disturbed D1	D2	median	min – max
Geometridae								
Ennominae	0.40	0.41	0.49	0.42 – 0.57	0.43	0.39	0.54	0.43 – 0.64
Larentiinae	0.41	0.45	0.40	0.31 – 0.45	0.43	0.53	0.33	0.24 – 0.42
Sterrhinae	0.10	0.08	0.06	0.03 – 0.07	0.08	0.06	0.06	0.02 – 0.10
Geometrinae	0.09	0.06	0.06	0.04 – 0.08	0.06	0.03	0.07	0.04 – 0.10
Ennominae								
Azelinini	0.15	0.14	0.04	0.02 – 0.06	0.12	0.09	0.02	0.01 – 0.04
Boarmiini	0.08	0.10	0.14	0.10 – 0.25	0.09	0.18	0.18	0.08 – 0.46
Caberini	0.08	0.07	0.07	0.05 – 0.14	0.04	0.07	0.05	0.04 – 0.18
<i>Cratoptera</i> group	0.02	0.05	0.05	0.01 – 0.07	0.01	0.02	0.02	0.01 – 0.05
Macariini	0.02	0.03	0.01	0.01 – 0.04	0.01	0.01	0.02	0.00 – 0.03
Nacophorini	0.06	0.02	0.05	0.03 – 0.08	0.06	0.04	0.05	0.03 – 0.11
Nephodiini	0.08	0.07	0.11	0.05 – 0.17	0.05	0.03	0.11	0.05 – 0.18
Ourapterygini	0.19	0.24	0.16	0.12 – 0.21	0.12	0.25	0.14	0.08 – 0.19
Palyadini	0.02	0.03	0.05	0.02 – 0.07	0.01	0.01	0.03	0.01 – 0.11
Rest	0.29	0.24	0.31	0.25 – 0.34	0.50	0.29	0.26	0.20 – 0.42
Larentiinae								
<i>Eois</i>	0.16	0.14	0.22	0.15 – 0.41	0.10	0.06	0.28	0.15 – 0.48
<i>Eupithecia</i>	0.44	0.42	0.33	0.20 – 0.48	0.58	0.47	0.30	0.18 – 0.50
<i>Psaliodes</i>	0.10	0.18	0.21	0.14 – 0.27	0.09	0.18	0.18	0.12 – 0.42
Rest	0.30	0.26	0.20	0.12 – 0.22	0.23	0.29	0.15	0.07 – 0.28

information on proportions of different taxa (species, individuals) at the disturbed sites as well as median, minimum and maximum values of the ten forest sites. Specimen proportions do not always perfectly reflect patterns of species proportions, but never show contrasting results.

The species proportion of the large subfamily Ennominae at the disturbed sites is lower than that of all forest sites. This is counterbalanced by higher proportions of Sterrhinae and Geometrinae (D1 only). Specimen proportions of ennomines are also lower at the disturbed sites, whereas more larentiine individuals occur.

Within Ennominae, significantly larger species and specimen proportions of the tribes Azelinini and Ourapterygini (D2 only) are found in disturbed habitats compared with forest sites (Table 1). On the other hand, species of the tribe Boarmiini tend to be underrepresented, with lower values at the disturbed sites compared with the median proportion of the forest sites. Specimens not assigned to genera are overrepresented at site D1. The ennomine genus *Bonatea* (Nephodiini) and the *Herbita* complex (not assigned to tribe) are conspicuously absent at the disturbed sites whereas they occur rather abundantly at the forest plots, with four and six species respectively (Brehm 2002). Other taxa such as two

species of *Pantherodes* (not assigned to tribe) occur in abundance at the disturbed sites and are less common in the forest.

In Larentiinae, species of the very species-rich genus *Eois* are represented by only 14–16% at the two disturbed habitats. Such a low percentage can only be found at one of the highest forest sites (7b: 15%), whereas the median of the proportion of *Eois* species at the forest sites is 22%. The number of *Eois* specimens is also very low compared with forest sites. Higher proportions of other larentiine taxa counterbalance this low proportion of *Eois* species and specimens. The genus *Eupithecia* dominates the larentiine ensembles of the disturbed sites as it does at the uppermost forest plots. However, trends within Larentiinae (*Psaliodes*, remaining genera) are not fully consistent. All four species of the genus *Hagnagora* found in Brehm's (2002) study were also collected at the disturbed sites.

Ensembles from disturbed sites are characterized by a moderate loss of diversity (see above) and by a low number of species exclusive to these habitats. Only a moderate number of species that also occur in forest profits from disturbance, and species dominance was low like at the forest sites.

Among the 197 species found at the disturbed sites, only 20 (10%) were not detected in the forest

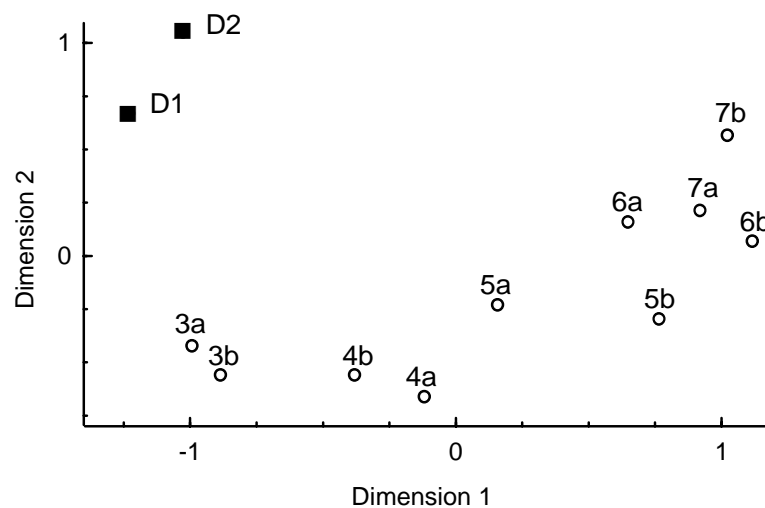


Fig. 3. Non-metric two-dimensional scaling of samples of geometrid moths from two disturbed and ten undisturbed forest sites in southern Ecuador. The ordination is based on the CNESS index with its sample size parameter m set to an intermediate value of 36 (stress: 0.05).

(‘exclusive’ species, Appendix 1). Most of these species were rare: twelve species with one specimen each, and five species with a total of two specimens. One species was collected with a total of three specimens (*Eupithecia densicauda*), one with six (*Pero obtusaria*), and one with seven (*Sabulodes muscistrigata*). Two species were common at the disturbed sites as well as at the forest sites at elevational level 3 (*Sabulodes thermidora*, *Perizoma emmelesiata*). Other species were found in larger numbers compared with forest habitats (figures printed in bold in Appendix 1). These species include (singletons and doubletons discarded): *Budara partita*, *Pantherodes colubraria viperaria*, *P. conglomerata*, *Perissopteryx* sp.nr. *nigricomata*, *Pero semiusta*, *Perusia verticata* (Ennominae), *Euphyia aguada*, *Eupithecia duena*, *E. lachaumei*, *E. sp.nr. penicilla*, *Eupithecia* sp., *E. yangana*, *Orthonama effluata*, *Psaliodes inundulata* (Larentiinae) and *Tricentrogyna collustrata* (Sterrhinae).

The two-dimensional scaling (Figure 3), based on the CNESS index ($m = 36$), shows an arrangement of the ten forest sites roughly according to their elevational order. Appendix 2 provides the original dissimilarity matrix. As in previous studies (Brehm et al. 2003a), extracted scores of the first dimension of the forest plots correlate highly significantly with the altitude of the sites ($r^2 = 0.87$, $P < 0.001$). In contrast, the two disturbed sites are not arranged according to their elevational position. Rather, they are separated by having lower scores in the first dimension and higher scores in the second dimension than all the forest sites.

DISCUSSION

Possible causes for the high alpha diversity

Anthropogenic disturbance in the study area causes a strong decline in plant diversity (J. Homeier, personal communication). It also leads to a decrease of certain important food resources, such as soft-leaved herbs and understorey shrubs (Paulsch 2002), and to a fundamental change of microclimatic conditions. We therefore expected a significant decline of geometrid diversity as shown e.g. by Beck et al. (2002) in Borneo. However, the results show that local diversity is surprisingly high at disturbed sites, but tends to be lower compared with the forest sites. Values of Fisher’s alpha larger than 86 are still

far beyond those recorded from any temperate site and are among the highest in the world. The values for the extrapolated species number gives an impression of the order of magnitude of actual richness between 200 and 300 species while the results for rarefied species are arranged according to those of the other two measures.

The high diversity of geometrid moths found at the disturbed sites can be explained by (1) suitability of disturbed habitat, and (2) dispersal from adjacent habitats. Disturbed sites in the study area might offer appropriate habitats for a number of species using plants of early successional stages as larval food resources. Lepš et al. (2001) stated that tropical successions could represent a suitable habitat for many insects. In particular, degraded forest remnants might offer a still wider range of resources. On the contrary, open landslides, cattle pastures and bracken fallows provide an extremely impoverished set of potential hosts. It is likely that the dispersal of ‘tourist species’ from adjacent forest sites plays an important role, and that the diversity of the disturbed sites might be overestimated due to this phenomenon. The high number of species represented by only one individual might also indicate an increased proportion of species that only pass through. However, a high rate of singletons is a typical feature of incompletely sampled tropical arthropod communities (Novotny & Basset 2000). Holloway et al. (1992) found that samples from plantations located in the vicinity of secondary forest contained a considerable component of that fauna. Many of the species depended on plants that were not present in the plantation. Thomas (2002) interpreted high values of Fisher’s alpha of geometrid moths at a clearcut site in a Canadian red spruce forest as the consequence of the dispersal of tourist species from unlogged forest. Ricketts et al. (2001) found a relatively high species richness and abundance of moths around forest fragments in Costa Rica. They described the phenomenon as moth ‘halos’ extending more than one kilometer from the forest edge. The disturbed sites in our study area lay within this range (ca. 0.5 km). It is unlikely that moths were attracted from far away by the light-traps, since our study, and those of Ricketts et al. (2001) and Thomas (2002) were conducted with very weak light sources (30, 12, and 22 W, respectively). In order to minimize edge and dispersal effects in further studies, we recommend a study design with large distances between sites which are situated in homogeneous habitats.

Changes in ensemble structure

Some conspicuous patterns have emerged with regard to structure and species composition of the ensembles from the disturbed habitats. The species proportion of the very species-rich genus *Eois* is significantly lower at disturbed sites than at those in the forest, and all twelve species at the disturbed sites were collected only in low numbers (maximum 4, Appendix 1). All known Neotropical *Eois* larvae are specialized feeders on *Piper* species (Brehm 2002, Dyer et al. 2003, L. Dyer & D.L. Gentry, personal communication). Herbs and shrubs of this family are an important component of the understorey within the intact forest whereas this resource is largely absent at disturbed sites (J. Homeier, personal communication). Another conspicuous pattern is the absence of the large-bodied ennomine genera *Bonatea* and *Herbita* which also might be associated with missing hostplants. However, available host plant data are still too few for a clear interpretation.

The three more abundant exclusive species *Eupithecia densicauda*, *Pero obtusaria* and '*Sabulodes muscistrigata*' might be regarded as typical components of disturbed habitat, but stochastic sampling effects are likely to play a major role for the remaining exclusive species. The two species common at the disturbed sites as well as at the forest sites at elevational level 3 (*Sabulodes thermidora*, *Perizoma emmelesiata*) could be dispersers from open landscape because these sites are situated at the forest edge.

The high number of species of the genus *Eupithecia* is noticeable, and can be explained by the availability of suitable hosts in disturbed habitats. It is probable that most of these moths had actually developed in disturbed habitats, since Brehm (2003) found larvae of *Eupithecia* of several species in different successional stages on host plants such as the shrub *Baccharis latifolia* (Asteraceae). Species of the larentiine genus *Hagnagora* were represented by all four species listed by Brehm (2002) from intact forest. At least two of these species were recorded on *Clethra* hostplants. *C. revoluta* is a common plant in the study area and occurs together with two other *Clethra* species on early successional stages (J. Homeier, personal communication). Other obviously generalist species were common at both disturbed and forest sites. Examples include *Microxydia* sp. nr. *ruficomma*, *Physocleora pulverata*, *Euphyia subguttaria*, *Perizoma zenobia*, *Psaliodes catenifera*, *P. albifascia*, and *Idaea recrenita*.

Against expectations, dominance was low at disturbed sites. The most common species were *Eupithecia yangana* and *Sabulodes thermidora* at site D1 (Berger-Parker index: 5.8%), and *Psaliodes inundulata* at site D2 (Berger-Parker index: 7.9%). This falls within the range of the generally low dominance values of geometrid moths at the forest sites (median 6.7, minimum 4.9, maximum 19.0%). The result stands in contrast to studies showing higher dominance values of ensembles at disturbed habitats, e.g. of geometrid moths in Borneo (Beck et al. 2002).

In the ordination, geometrid ensembles from the two disturbed sites are separated from those at forest sites (Figure 3). On the first axis, ensembles of disturbed sites are not ordinated according to their elevational position as are the forest plots, but are ordinated 'too low'. This result is confirmed when additional ensembles from lower elevations (1380 m, Brehm 2002) are included in the ordination (unpublished results). The pattern might reflect an elevational shift of disturbance ensembles because open habitats could potentially provide warmer conditions as compared to forest habitats. Another explanation is the geographical proximity of sites D1 and D2 to forest sites at elevational levels 3 and 4 (Figure 1). There is a higher chance of dispersal from these nearer plots compared to forest sites at larger distances apart. Further studies could reveal whether physiological adaptations of moth species or geographical proximity of sites play the more important role for the shift along the first dimension. The second dimension might be interpreted as a gradient of 'openness' of vegetation, because trees become smaller and vegetation becomes less dense with rising elevation (Homeier et al. 2002, Paulsch 2002) as well as with rising levels of disturbance.

CONCLUSIONS

The relatively high diversity of geometrid moths at disturbed sites is probably due to the suitability of secondary forest remnants as habitat and also to the role of immigrating species from adjacent intact forest. However, the diversity of some specialized feeders declined, and disturbed sites added only little to the local species-pool because 90% of the species found at disturbed sites are also present at forest sites. More host plant information is required in order to learn more about the responses of Neotropical moths to

habitat changes. Inventories of caterpillars and their host plants in north-western Costa Rica (D. Janzen, W. Hallwachs et al.) and in northern Ecuador (L. Dyer, D.L. Gentry, H. Greeney et al.) provide such important ecological data.

Our results provide a first impression of the effects of habitat disturbance on a highly diverse arthropod group in a montane rainforest in the Andes. Continuing from this, further studies should investigate the response of geometrid moths to different levels of disturbance and land-use, such as selective logging or the transformation of forest into cattle pasture and plantations in the Andes. The ongoing destruction of Andean rainforests could well have a severe impact on the diversity of geometrid moths. Given that the Andean rainforests are the worldwide hotspot of diversity for Geometridae (Brehm 2002), and for a range of other organisms (e.g. Myers et al. 2000), there is obviously reason for concern from a conservation viewpoint. Strong measures should be taken in order to protect the remaining pristine and secondary habitats.

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APPENDICES

Appendix 1

List of 197 geometrid moth species collected at two sites of disturbed montane habitats in southern Ecuador. Taxonomy follows Pitkin (2002) for Ennominae, and Scoble (1999) for the remaining Geometridae. Taxon numbers refer to data base numbers that are largely identical to the list of species provided by Brehm (2002). Some taxonomic changes have been performed since Brehm's (2002) study because a number of species have been identified in the meantime in the BMNH, USNM and AMNH collections. The column 'exclusive' refers to those species that were not collected by Brehm (2002) in montane forest habitats. Twenty species were collected exclusively at the disturbed sites. sp nr = species near, but not identical with a described species. Numbers printed in bold are those which exceed specimen numbers sampled at any of the 22 forest sites analyzed by Brehm (2002).

Taxon number	Species	D1	D2	exclusive
Ennominae				
292	<i>'Apiciopsis' maciza</i> Dognin	-	1	
73	<i>Argyrotome prospectata</i> Snellen	-	1	
53	<i>Bassania goleta</i> Dognin	-	3	
268	<i>Bryoptera friaria</i> Schaus	1	-	
779	<i>Bryoptera</i> sp nr <i>friaria</i> Schaus	-	1	
774	<i>Budara partita</i> Warren	3	1	
357	<i>Cargolia toulgoeti</i> Herbulot	1	-	x
95	<i>Certima lojanata</i> Dognin	1	1	
253	<i>Certima miligina</i> Dognin	-	1	
90	<i>Cimicodes</i> sp	2	-	
291	<i>Cirsodes casta</i> Warren	-	1	
1040	<i>Cirsodes macilentata</i> Guenée	-	1	
52	<i>Eusarca</i> sp	-	1	x
265	<i>Glena</i> sp nr <i>juga</i> Rindge	-	1	
88	<i>Herbita decurtaria</i> Herrich-Schäffer	-	1	
257	<i>Iridopsis gaujoni</i> Prout	-	1	
256	<i>Iridopsis</i> sp nr <i>subnigrata</i> Warren	3	-	
112	<i>Isochromodes extimaria</i> Walker	2	-	
98	<i>Isochromodes polvoreata</i> Dognin	-	1	
102	<i>Isochromodes</i> sp	-	1	
105	<i>Isochromodes</i> sp	1	2	
106	<i>Isochromodes</i> sp	4	4	
302	<i>Leuculopsis bilineata</i> Warren	-	2	
1030	<i>Leucula</i> sp nr <i>ablinearia</i> Guenée	1	-	
192	<i>Lomographa tributaria</i> Walker	1	1	
768	<i>Macaria lydia</i> Schaus	-	1	
172	<i>Macaria lapidata</i> Warren	1	-	
180	<i>Mesedra</i> sp	1	-	
974	<i>Melanolophia musarana</i> Dognin	1	1	x
695	<i>Microxydia</i> sp nr <i>ruficomma</i> Prout	7	-	
166	<i>Mychonia corticinaria</i> Herrich-Schäffer	1	-	
546	<i>Mychonia</i> sp	-	1	x
170	<i>Neazata fragilis</i> Warren	1	-	
861	<i>Narragodes ochreatea</i> Dognin	2	-	x
286	<i>Neodora glaucularia</i> Snellen	-	4	
810	<i>Nephodia clara</i> Dognin	-	1	
216	<i>Nephodia pardata</i> Dognin	1	-	
211	<i>Nephodia occulta</i> Warren	-	1	

Taxon number	Species	D1	D2	exclusive
142	<i>Oenoptila</i> sp nr <i>recessa</i> Dognin	-	1	
232	<i>Opisthoxia</i> sp nr <i>danaeata</i> Walker	1	1	
59	<i>Oxydia</i> <i>augusta</i> Druce	-	1	
60	<i>Oxydia</i> <i>geminata</i> Maassen	1	2	
71	<i>Oxydia</i> <i>optima</i> Dognin	-	2	
72	<i>Oxydia</i> <i>scriptipennaria</i> Walker	1	1	
58	<i>Oxydia</i> <i>trychiata</i> Guenée	1	12	
297	<i>Pantherodes</i> <i>colubraria viperaria</i> Thierry-Mieg	5	13	
298	<i>Pantherodes</i> <i>conglomerata</i> Warren	4	5	
162	<i>Periclina</i> <i>rumiaria</i> Guenée	-	1	
154	<i>Perissopteryx</i> sp nr <i>nigricomata</i> Warren	1	7	
947	<i>Pero</i> <i>algerna</i> Schaus	-	1	
239	<i>Pero</i> <i>buckleyi</i> Butler	3	1	
248	<i>Pero</i> <i>caustomeris</i> Prout	-	1	
472	<i>Pero</i> <i>obtusaria</i> Schaus	3	3	x
245	<i>Pero</i> <i>periculosaria</i> Oberthür	1	-	
924	<i>Pero</i> <i>pretensa</i> Poole	1	-	
928	<i>Pero</i> sp	-	1	x
833	<i>Pero</i> sp nr <i>semiusta</i> Butler	3	4	
791	<i>Pero</i> <i>spectrata</i> Felder & Rogenhofer	-	1	
247	<i>Pero</i> <i>tricararia</i> Poole	1	-	
793	<i>Pero</i> <i>tridenta</i> Poole	1	-	x
792	<i>Pero</i> <i>unfortunata</i> Poole	-	1	
328	<i>Perusia</i> <i>verticata</i> Warren	3	3	
327	<i>Perusia</i> <i>viridis</i> Warren	-	1	
147	' <i>Petelia</i> ' <i>anagogaria</i> Warren	-	1	
630	' <i>Petelia</i> ' sp	1	-	x
49	<i>Phyllodonta</i> <i>caninata</i> Guenée	1	-	
137	<i>Phyllodonta</i> <i>muscilinea</i> Guenée	1	-	
46	<i>Phyllodonta</i> sp nr <i>flabellaria</i> Thierry-Mieg	1	1	
334	<i>Physocleora</i> <i>mniophilaria</i> Guenée	-	1	
333	<i>Physocleora</i> <i>pulverata</i> Warren	5	20	
318	<i>Pyrinia</i> <i>gallaria</i> Walker	1	-	
317	<i>Pyrinia</i> <i>megara</i> Druce	3	3	
309	<i>Rucana</i> <i>abnormipalpis</i> Warren	1	-	
311	<i>Rucana</i> <i>degener</i> Warren	5	6	
122	<i>Sabulodes</i> sp nr <i>carbina</i> Druce	2	1	
125	<i>Sabulodes</i> <i>thermidora</i> Thierry-Mieg	21	3	
873	' <i>Sabulodes</i> ' <i>musciatrigata</i> Guenée	4	3	x
175	<i>Semiothisa</i> <i>radiata</i> Maassen	-	1	
202	<i>Sericoptera</i> <i>mahometaria</i> Herrich-Schäffer	1	2	
281	<i>Stenalcidia</i> <i>celosoides</i> Dognin	-	1	
275	<i>Stenalcidia</i> sp nr <i>delgada</i> Dognin	1	-	
Geometrinae				
761	<i>Lissochlora</i> <i>cecilia</i> Prout	-	1	
351	<i>Lissochlora</i> <i>hoffmannsi</i> Prout	2	-	
352	<i>Lissochlora</i> <i>latuta</i> Dognin	2	1	
355	<i>Nemoria</i> <i>aturia scotocephala</i> Prout	1	1	
345	<i>Nemoria</i> <i>nigrisquama</i> Dognin	2	-	
349	<i>Nemoria</i> sp nr <i>sellata</i> Warren	1	-	
882	<i>Nemoria</i> sp nr <i>erina</i> Dognin	-	1	x
344	<i>Oospila</i> <i>ecuadorata</i> Dognin	1	-	
360	<i>Phrudocentra</i> <i>subaurata</i> Warren	2	1	
341	<i>Poecilochlora</i> <i>minor</i> Warren	1	-	
342	<i>Rhodochlora</i> <i>roseipalpis</i> Felder & Rogenhofer	1	1	
347	<i>Synchlora</i> <i>amplimaculata</i> Herbulot	1	2	
350	<i>Synchlora</i> <i>gerularia</i> Hübner	-	1	
611	<i>Synchlora</i> <i>dependens tumefacta</i> Warren	2	1	
Larentiinae				
391	<i>Eois</i> <i>amarillada</i> Dognin	1	2	
1033	<i>Eois</i> <i>apyraria</i> Guenée	-	1	x
392	<i>Eois</i> <i>chasca</i> Dognin	1	1	
1029	<i>Eois</i> <i>chrysocraspedata</i> Warren	2	1	
378	<i>Eois</i> <i>encina</i> Dognin	-	1	
803	<i>Eois</i> <i>muscosa</i> Dognin	1	-	
387	<i>Eois</i> <i>nigricosta</i> Prout	-	1	

Taxon number	Species	D1	D2	exclusive
404	<i>Eois obada</i> Druce	1	-	
416	<i>Eois olivacea</i> Felder & Rogenhofer	1	2	
424	<i>Eois paraviolascens</i> Dognin	3	1	
419	<i>Eois</i> sp nr <i>odatis</i> Druce	1	-	
961	<i>Eois</i> sp nr <i>tegularia</i> Guenée	-	1	
482	<i>Euphyia aguada</i> Dognin	4	5	
952	<i>Euphyia infundibulata</i> Guenée	-	2	
633	<i>Euphyia psyra</i> Druce	1	1	
465	<i>Euphyia</i> sp	1	-	
462	<i>Euphyia</i> sp nr <i>fringillata</i> Guenée	-	3	
460	<i>Euphyia subguttaria</i> Herrich-Schäffer	1	4	
813	<i>Euphyia violetta</i> Warren	3	1	
623	<i>Eupithecia anita</i> Warren	2	3	
554	<i>Eupithecia casta</i> Warren	-	2	
512	<i>Eupithecia densicauda</i> Warren	2	1	x
559	<i>Eupithecia disformata</i> Dognin	-	1	
556	<i>Eupithecia duena</i> Dognin	3	15	
677	<i>Eupithecia higa</i> Dognin	3	1	
679	<i>Eupithecia hilaris</i> Prout	1	1	
569	<i>Eupithecia hormiga</i> Dognin	2	-	
563	<i>Eupithecia lachaumei</i> Herbulot	9	11	
661	<i>Eupithecia nigrithorax</i> Warren	3	-	
653	<i>Eupithecia nigrodiscata</i> Herbulot	-	2	
562	<i>Eupithecia penicilla</i> Dognin	-	2	
550	<i>Eupithecia rubellicincta</i> Warren	2	4	
674	<i>Eupithecia sobria</i> Prout	3	-	
580	<i>Eupithecia</i> sp	-	1	
586	<i>Eupithecia</i> sp	-	1	
926	<i>Eupithecia</i> sp	-	1	x
604	<i>Eupithecia</i> sp	2	8	
609	<i>Eupithecia</i> sp	2	2	
622	<i>Eupithecia</i> sp	-	2	
624	<i>Eupithecia</i> sp	-	2	
645	<i>Eupithecia</i> sp	3	5	
646	<i>Eupithecia</i> sp	1	-	
658	<i>Eupithecia</i> sp	1	-	
664	<i>Eupithecia</i> sp	1	-	
666	<i>Eupithecia</i> sp	-	2	
876	<i>Eupithecia</i> sp	1	2	
900	<i>Eupithecia</i> sp	1	-	
572	<i>Eupithecia</i> sp nr <i>contexta</i> Schaus	1	-	
574	<i>Eupithecia</i> sp nr <i>contexta</i> Schaus	1	1	
561	<i>Eupithecia</i> sp nr <i>penicilla</i> Dognin	2	9	
615	<i>Eupithecia</i> sp nr <i>saphenes</i> Prout	-	1	
555	<i>Eupithecia</i> sp nr <i>sobria</i> Prout	-	1	
570	<i>Eupithecia versiplaga</i> Warren	-	1	
667	<i>Eupithecia yangana</i> Dognin	21	9	
435	<i>Hagnagora anicata</i> Felder & Rogenhofer	-	2	
434	<i>Hagnagora croceitincta</i> Dognin	-	1	
433	<i>Hagnagora ephestris</i> Felder & Rogenhofer	1	1	
436	<i>Hagnagora mortipax</i> Butler	1	-	
468	<i>Hammaptera praderia</i> Dognin	1	-	
469	<i>Hammaptera</i> sp	2	-	
475	<i>Hydriomena</i> sp nr <i>cydra</i> Druce	1	2	
951	<i>Obila umbrinata</i> Guenée	1	-	
441	<i>Orthonama effluata</i> Snellen	3	7	
492	<i>Perizoma basiplaga</i> Schaus	-	1	
486	<i>Perizoma emmelesiata</i> Snellen	1	14	
487	<i>Perizoma zenobia</i> Thierry-Mieg	5	3	
894	<i>Pocophora rufisticta</i> Warren	-	1	x
489	<i>Psaliodes albifascia</i> Dognin	2	2	
524	<i>Psaliodes castanea</i> Warren	-	1	
496	<i>Psaliodes catenifera</i> Warren	3	1	
539	<i>Psaliodes cedaza</i> Dognin	1	1	
538	<i>Psaliodes confusa</i> Warren	-	1	
532	<i>Psaliodes crassinota</i> Dognin	-	2	
488	<i>Psaliodes inundulata</i> Guenée	3	21	
698	<i>Psaliodes nictitans</i> Warren	-	1	
541	<i>Psaliodes perfuscata</i> Bastelberger	-	2	
501	<i>Psaliodes</i> sp	1	-	

Taxon number	Species	D1	D2	exclusive
499	<i>Psaliodes</i> sp nr <i>endotrichiata</i> Snellen	-	6	
393	<i>Psaliodes</i> sp nr <i>philetus</i> Schaus	-	1	x
518	<i>Psaliodes strigosa</i> Warren	-	1	
33	<i>Scotopteryx fulminata</i> Dognin	-	1	
513	<i>Smileuma plagifracta</i> Prout	-	1	
440	<i>Triphosa affirmata</i> Guenée	1	-	
Sterrhinae				
29	<i>Cyclophora acutaria</i> Walker	-	1	
8	' <i>Cyclophora</i> ' <i>gracilinea</i> Warren	-	1	
11	' <i>Cyclophora</i> ' <i>lancearia</i> Felder & Rogenhofer	-	1	
36	<i>Idaea arhostiodes</i> Warren	1	-	
40	<i>Idaea fimbriata</i> Warren	-	1	
41	<i>Idaea quadrirubata</i> Warren	-	1	
34	<i>Idaea reclinata</i> Prout	3	2	
35	<i>Idaea</i> sp nr <i>iridaria</i> Schaus	2	-	
38	<i>Lobocleta costalis</i> Dyar	1	-	
972	<i>Pleuroprucha</i> sp	1	-	
880	<i>Scopula privata</i> Walker	2	-	x
704	<i>Scopula</i> sp	1	-	x
595	<i>Scopula</i> sp	1	1	x
987	<i>Scopula</i> sp	2	-	x
27	<i>Scopula</i> sp nr <i>subquadrata</i> Guenée	-	1	
23	<i>Semaepus dentilinea</i> Warren	1	-	
21	<i>Semaepus verbena</i> Dognin	-	1	
42	<i>Tricentrogyna collustrata</i> Snellen	5	10	
39	<i>Tricentrogyna nigricosta</i> Warren	1	1	

Appendix 2

Dissimilarity matrix based on the CNESS index ($m = 36$) for two disturbed sites and ten undisturbed sites of montane rainforest in southern Ecuador. Note that CNESS may attain a potential maximum of the square root of 2 = 1.414.

	3a	3b	4a	4b	5a	5b	6a	6b	7a	7b	D1
3b	0.68	0									
4a	1.03	1.04	0								
4b	0.93	0.99	0.75	0							
5a	1.06	1.03	0.89	0.98	0						
5b	1.19	1.16	1.01	1.07	0.83	0					
6a	1.17	1.13	1.04	1.11	0.91	0.82	0				
6b	1.25	1.23	1.11	1.14	1.01	0.94	0.77	0			
7a	1.19	1.10	1.13	1.13	1.00	0.95	0.73	0.74	0		
7b	1.23	1.21	1.18	1.17	1.05	0.99	0.77	0.88	0.78	0	
D1	1.07	1.08	1.16	1.13	1.14	1.22	1.20	1.26	1.22	1.25	0
D2	1.12	1.17	1.16	1.16	1.18	1.21	1.20	1.25	1.22	1.24	0.83