Functional biodiversity and climate change along an altitudinal gradient in a tropical mountain rainforest

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Summary

This article investigates possible consequences of climate change for a hotspot of tropical biodiversity, exemplified by a comparatively small area of a neotropical mountain rain forest in the eastern range of the South Ecuadorian Andes. In the introduction, several approaches for such predictions are evaluated with respect to their applicability to the eco-region. After a short presentation of the research area and its biodiversity, climate and vegetation development during the Holocene is described showing the range of possible fluctuations between Puna-like grassland and tropical mountain forest. Data of climate dynamics during the past 50 – 60 years, covering several ENSO (El Niño Southern Oscillation) events, suggest a significant increase in temperature but no dramatic changes in the precipitation regimes of the region. Due to the altitudinal span of the area, the rise in temperature will shift the ecothermic belts by several hundred meters uphill and thus increase the distribution ranges of ectothermic organisms. To assess the consequences of this shift on biodiversity two model approaches were applied, namely the species-area-approach and the energetic-equivalence rule, using the extremely diverse insect group of moths. Combining both approaches the consequences of a climate change

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can be estimated for the various scenarios of greenhouse gas emissions published by the International Panel for Climate Change (IPCC 2007). Applying the most realistic scenario A1B a reduction of moth species by 31% until the year 2100 can be predicted for the RBSF area. Due to their greater life-span, woody plants are much more resilient to climate change, especially so in a megadiverse forest with usually small population sizes. Therefore impacts of global warming on the local vegetation can only be assessed on the basis of qualitative data of the forest structure rather than of the floristic composition. The most conspicuous trait of the tropical mountain rain forest in the region is the low elevation of the upper tree-line which on average is by 1000 to 1500 m lower than in the other parts of the tropical Andes. Due to the particular orographic situation, the extreme environmental conditions (quasi-permanent easterly storms carrying a tremendous load of precipitation) do not allow growth of trees in the peak regions of the mountains. Only if the prevailing trade-wind system would dampen and the mountain range would receive less precipitation a change of the environmental conditions can be expected resulting in a situation like in the early and mid Holocene, when a forest covered the entire mountain range. However, up to present, symptoms for such a change are lacking. A final outlook comments on the priority ranking of climate change vs. direct anthropogenic impacts with respect to conservation measures. For the investigated tropical forest ecosystem a reduction of human impact is more urgent than ever.

1 Introduction

Organisms react in different ways to climate change, (i) by thriving in a modifying climate through genetic adaptation, phenotypic plasticity, or ecological buffering, (ii) by migrating to areas with more proper climates, or (iii) by going extinct (Theurillat and Guisan 2001). Thus, the impact of climate change on biodiversity can result in species enrichment as postulated for many biomes of cooler climates (Thuiller 2004) as well as in species losses as predicted for most dry biomes and for parts of the wet tropics as well (Colwell et al. 2008). Williams et al. (2007) argued that climate conditions which favoured some of the biodiversity hotspots during the past century may entirely disappear during the 21th century. In that respect the biodiversity hotspot area of the tropical Andes will be most endangered (their Figs. 2 E and F). Climate changes can result in range-shifts and/or extinction of species, but may also be without substantial effects on species distribution patterns. For the first two assumptions the formation of novel organismic communities is obvious. Several approaches could be worth considering to predict effects of climate change on the biological diversity of an area:

- Modelling the species or group-specific responses to altered climatic conditions is one possibility to forecast future climatic impacts on biodiversity, though such predictions should be considered as first approximation, rather than as reliable prognoses (e.g. Pearson and Dawson 2003).

- Niche-theory models based on species – habitat relations represent a more sophisticated option for biodiversity perspectives (e.g. Thuiller et al. 2005). However, such Species Distribution Models (SDM) are based on the assumption that the observed distribution of a species is in equilibrium with its current habitat (Guisan and Thuiller 2005).
- Coupling the biosphere and pedosphere with Regional Atmospheric Modelling Systems Models (RAMS) may be of higher accuracy for developing biodiversity scenarios. Problems occur, if ecological systems comprise poorly quantifiable processes rendering the applicability of RAMS questionable (Botkin et al. 2007).
- Finally, species–area curve models that consider all species or at least large aggregates of species are also used in biodiversity research (Thomas et al. 2004). Nevertheless, various limitations of this approach for predicting climate change effects must be critically assessed (Lewis 2006).

Most of the mentioned models were developed in Europe and northern America and have been implemented for predicting biodiversity changes in cooler and temperate zones. Nearly all predictions for these comparatively simple-structured habitats anticipate partially dramatic species losses already during the current century. However, traits and processes that could preserve species diversity or even result in diversity enrichment remain largely unconsidered. Examples for that are biotic interactions, speed-up effects by fragmentation or (unpredictable) inputs by invasive species. Apart from the above mentioned particular limitations, the quoted approaches seem less useful for tropical biomes and especially not for ecosystems harboring biodiversity hotspots like a tropical mountain rain forest.

In contrast, the approach used in this paper for a tropical mountain rainforest attempts to integrate existing data and well investigated ecological processes into present theories and to combine them with own findings. Using established models, the species-area approach considers the elevational area attenuation in mountains as one of the major problems of the altitudinal shift of species distribution ranges. Another approach, the energetic-equivalence rule regards the possible expansion or attenuation, respectively, of a well investigated ectothermic insect group upon future warming. Possible changes in plant diversity patterns upon climate change will be discussed on the basis of ecotonal structures, biotic interrelations, triggers for species area shifts and extinction, disturbance regimes, and invasion of pioneer species. Since Botkin et al. (2007) state that more frequent use of fossil records would improve forecasting methods, pollen and charcoal records have also been included in this work.

2 The Study area and its biodiversity

The study site in southern Ecuador covers an area of around 100 km^2 in the valley of the Rio San Francisco, a tributary of the Rio Zamora. The site which partly belongs to the Podocarpus Nacional Parque has been studied since 1997 and a first comprehensive description of it has been published by Beck et al. (2008a). It encompasses a core area of 11 km^2 (termed Reserva Biológica San Francisco, RBSF, Fig. 1) and some smaller satellite areas. As part of the eastern range of the South Ecuadorian Andes, the entire region belongs to the tropical humid ecozone. From the North it reaches into an important ecological transition as well as border zone, the so-called Andean Depression. Separating the central and northern Andes, this orographic depression stretches 500 km N-S from the Girón-Paute drainage basin around Cuenca in southern Ecuador to the Rio Chicama-Rio Huallaga intersection around Cajamarca in northern Peru (Weigend 2002). Here, the Andes barely reach 4000 m and the tree line is as low as 3000 to 3400 m asl. Despite or just because of its low elevation, the Andean depression is considered an important biogeographical barrier. Especially its eastern escarpment harbours an important and fascinating centre of endemism (Young and Reynel 1997).

Global censuses of vascular plant biodiversity (Barthlott et al. 2007) identified five centres with diversity maxima of over 5000 vascular plant species per 10,000 km^2. In addition to the Costa Rica-Chocó area, south-eastern Brazil, northern Borneo and the New Guinea mountain range, the tropical Andes-Amazonia transition zone in Ecuador belongs to these five top megadiverse plant diversity hotspots. Within this large biogeographical zone, mountain rainforests because of their extraordinary biodiversity deserve particular attention (Beck and Richter 2008). Inventorying is still going on in the core and the total study area, but already until 2008 (Liede-Schumann and Breckle 2008, Brehm et al. 2008) 1208 seed plant species, 257 ferns and fern allies, 515 Bryophyta, 323 lichens, 83 Glomeromycota, and 96 Basidiomycota had been identified. Animal species inventories resulted in 21 bats, 379 birds, 243 butterflies (Papilionididae), 2396 moths (which is a world record), and representatives of several other arthropod groups.

3 Landscape history: Past vegetation, fire and climate dynamics

Knowledge of the landscape history is a prerequisite for the understanding of the emergence of a biodiversity hotspot. Comprehending the dynamics of the landscape is also necessary for appropriate management and conservation measures. Paleoecological studies in the Podocarpus National Park (PNP) region in the southern Ecuadorian Andes provide interesting insights into the dynamics of climate, vegetation, plant diversity, and the role of fire during the late Quaternary.

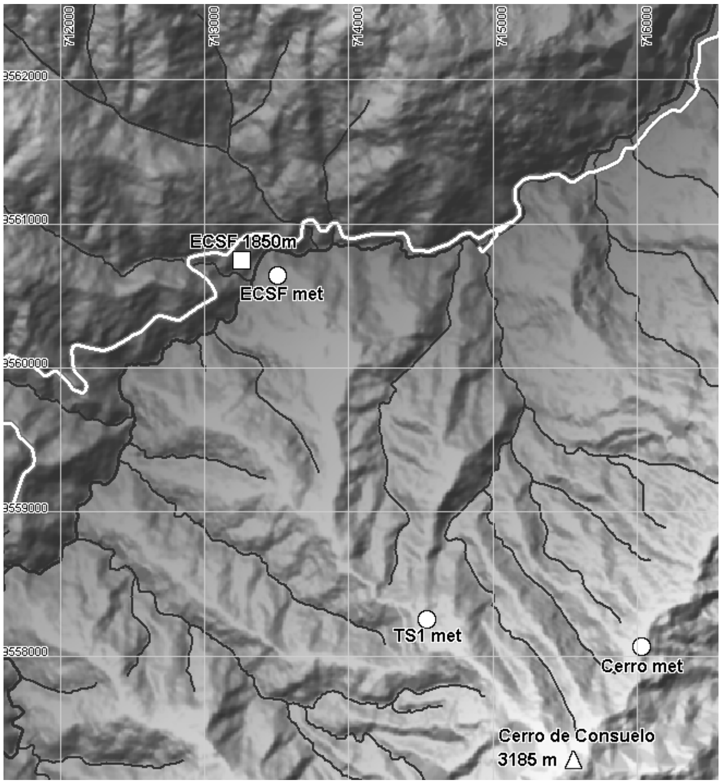

Fig. 1. Digital hill-shading image of the entire core study area that was used for the climate simulations. The connection road between Loja and Zamora is displayed in white, the river system in black, and "met" shows the sites of the meteorological stations. ECSF marks the location of the research station (Estación Científica San Francisco, lat. 3°58'18'' S, long. 79°4'45'' W, alt. 1,860 m a.s.l.). Cerro del Consuelo is the highest peak of the area. The river separating the north- and south-facing slopes is the Rio San Francisco. The research area corresponds to site # 4 in Fig. 10.

Studies have been carried out on a sediment core of a small bog at El Tiro pass (S 03°50'25.9'', W 79°08'43.2'', 2810 m elevation) in the eastern Cordillera, next to the road from Loja to Zamora near the ECSF research area (Niemann and Behling, 2008).

The study site is today covered by a shrubby subpáramo vegetation. The 17,000 yr BP (uncalibrated radiocarbon years before present) pollen record (Figs. 2 and 3) documents that grass páramo covered the region during the last glacial maximum (LGM) and Late-glacial periods. According to that record, only small populations of wind-pollinated tropical mountain forest trees occurred in the region, probably further down in the valley of the Rio San

Francisco. The tree line must have been markedly lower. The high frequency of *Plantago rigida* suggests wet climatic conditions in the Late-glacial period. From about 8000 to 3000 yr BP, i.e. in the early and mid Holocene, the former grass páramo was almost completely replaced by upper mountain rainforest, indicating drier and warmer climatic conditions than today. Woody genera, like *Hedyosmum, Symplocos*, and later *Myrsine*, *Ilex* and members of the Podocapaceae were much more common than at present. The warmer conditions are also reflected by the faster decomposition of the peat deposits compared to the late Holocene. Since the last 3000 years the area above 2780m a.s.l. is mainly covered by a shrubby subpáramo, dominated by species of the Melastomataceae.

The charcoal record shows that fires were rare during last glacial period and the early Holocene, until 8000 yr BP. Later on, fires became common on the slopes of El Tiro and further down. Three periods with increasing fire intensity could be identified: 8000 – 3000 yr BP, 2700 – 1800 yr BP and 1000 – 600 yr BP. During the last ca. 600 years fire frequency decreased again. The increased fire frequency during the wetter late Holocene suggests that fires were mostly of anthropogenic rather than of natural origin, e.g. lightning. It is assumed that the increasing use of slash-and-burn by humans settling in the drier valleys (e.g. in the Loja area) caused the spreading of fire into the mountains especially during the drier phases of the year. The decrease of common fern taxa including tree ferns can be interpreted as resulting from the effect of fire, in particular in the drier crest regions like El Tiro. The results underpin the notion that mountain ecosystems are quite sensitive to natural (climate) and anthropogenic impacts (fires).

In the El Tiro region as well as in the Cerro Toledo region (Brunschön and Behling, submitted) in the northern part of the Podocarpus Nacional Parque, mountain rainforest taxa were very rare or absent during the LGM. Sizable populations occurred only at lower elevations. Climatic conditions were cold and relatively wet and valleys above 3000 m elevation were probably glaciated. Present páramo islands were then connected to larger areas. Mountain rainforests accrued during the Late-glacial and in particular during the Holocene period, were markedly reduced and fragmented during cooler glacial periods. Connection and disconnection of various plant populations may have been an important component triggering speciation during the Quaternary (e.g. Hughes and Eastwood, 2006).

During the Late-glacial and, especially, the early Holocene mountain rainforests shifted up-mountain and developed, replacing the former grassland vegetation. The composition of the early to mid Holocene vegetation was different from that of the late Holocene. During early-mid Holocene, upper mountain rainforest was predominant at the coring site and the ample decomposition of organic material during that time suggests relatively warm and also somewhat drier conditions.

Tree populations have expanded their areas to higher elevations and replaced the existing páramo vegetation. However, in the Andean Depression, uplifting of habitat boundaries was limited by the relatively low elevation of the mountains. Nevertheless the areas covered now by subpáramo must have supported growth of trees at the early and middle Holocene. Today, the crest areas are subjected to nearly permanent strong easterly winds which allow growth of small trees only in hollows and small depressions. It must be concluded that during the early mid Holocene the wind regime and speed was different from the recent conditions.

Present-day vegetation became established after ca. 3000 yr BP, when the climate again became somewhat cooler and wetter. Major vegetation changes after 3000 yr BP have also been recorded in the Amazon lowland, where Amazonian rainforest expanded northwards and southwards of the equator (Behling and Hooghiemstra 2000, 2001, Mayle et al. 2000). This supports the hypothesis that changes in the climate regime of the Amazon lowland influenced the mountain rainforest of the eastern Andes.

4 Recent climate changes and area impacts

4.1 Recent climate dynamics

Figure 4 reveals the recent climate dynamics (1948-2005) for the grid cell of southern Ecuador using the NCEP/NCAR[5] reanalysis data, which encompass the RBSF study area (for data refer to Kistler et al. 2001). The plot shows a clear increase of the annual average air temperature over the last 57 years which runs parallel to the globally observed increase in atmospheric CO_2-concentration. The warming trend since 1948 yields 1.3°C, which means +0.22°C per decade. Quasi-periodic oscillations in air temperature are related to El Niño (EN, positive temperature anomalies) and La Niña (LN, negative temperature anomalies) events. No clear trend in rainfall exists in the data set. Also EN and LN years are not characterized by marked rainfall anomalies.

Generally, meteorological data from stations in the wider region confirm the reanalysis results for southern Ecuador (Fig. 5). The time series of air temperature at the station Loja (1950-2006), ˜30 km west of the ECSF meteorological station on the western side of the main Cordillera, reveals a warming trend of ˜0.6°C over the last 43 years (0.14°C per decade), somewhat lower than in the NCEP/NCAR data set. EN and LN show the same tendencies as in the NCEP/NCAR data set.

Also in the wider region no significant trend in rainfall can be recognized. However, a slight positive trend for the region west of the main cordillera (Loja) opposes a minimal decrease on the eastern escarpment at Zamora for the period 1963-1993. These tendencies on a first glance reflect the strong difference in climate dynamics along the short horizontal distance east and

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[5] *N*ational *C*enters for *E*nvironmental *P*rediction / *N*ational *C*enter of *A*tmospheric *R*esearch

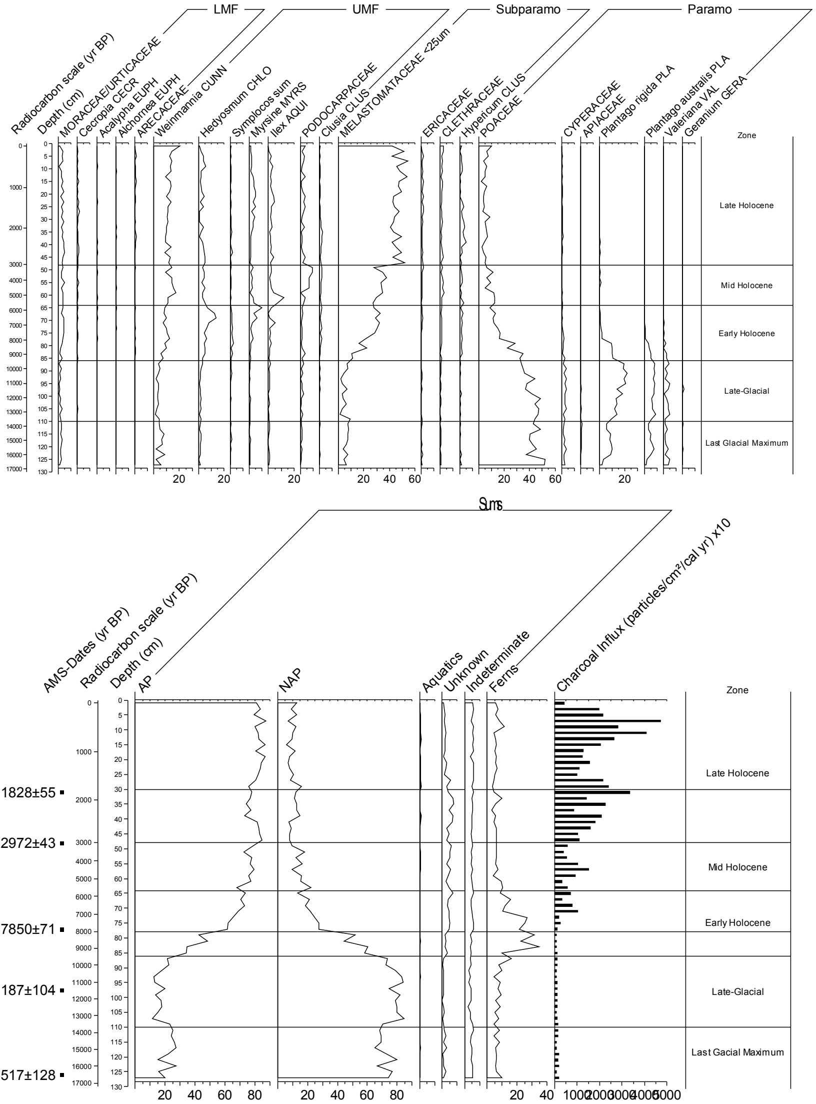

Fig. 2. Percentage pollen diagram of El Tiro in the southeastern Andes of Ecuador including selected taxa of lower mountain forest (LMF), upper mountain forest (UMF) subpáramo and páramo.

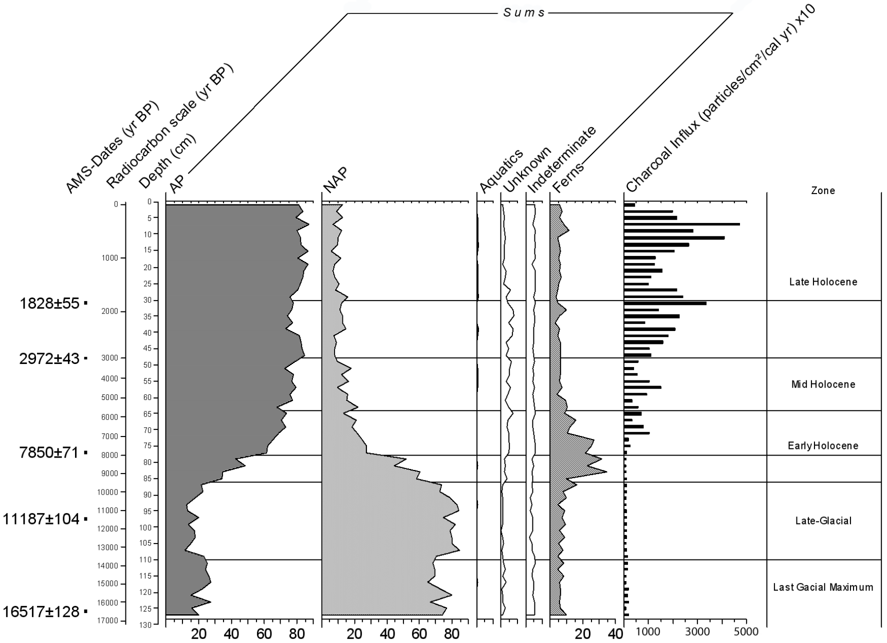

Fig. 3. Summary pollen diagram of El Tiro at 2810 m a.s.l.

west of the main cordillera (refer to Bendix et al. 2008b). Considering only one of these sites, e.g. the closest rainfall station (San Ramon) ~1 km down-valley the ECSF with a longer record reveals no trend in rainfall between 1980 and 2000.

Only 10 years of meteorological data are available from the core study site recorded by the meteorological stations shown in Fig. 1 (see Bendix et al. 2008a). Indeed, the years from 1999-2006 show generally the same warming trend in the upper part of the study area at the Cerro met station as in Loja ($r^2 = 0.56$ with Loja temperature data). This means that the warming trend is most probably the clearest local signal in climate development of global climate change.

4.2 Areal impacts of a projected climate change

The most likely forecast of the climate towards the end of the current century can be derived from the A1B scenario of greenhouse gas emission development until the year 2100 (see appendix). In spite of an expanding use of renewable sources of energy and a moderate economic growth, a fourfold increase of greenhouse gas emissions by 2100 relative to the pre-industrial level is predicted by thus model. For the grid cell of southern Ecuador, only a slight

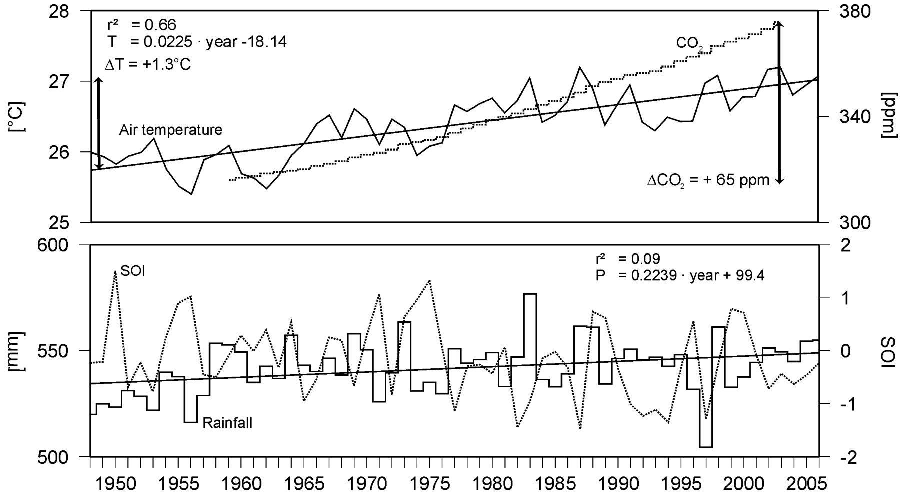

Fig. 4. NCEP/NCAR reanalysis data, average air temperature and rainfall totals for the grid cell of southern Ecuador (long. 3-6°S; lat. 76-79°E); CO_2-concentrations at NOAA-Mauna Loa observatory, Hawaii; Southern Oscillation Index SOI (source: NOAA); negative SOI represent warm phase conditions (El Niño like), positive SOI indicate cold phase conditions (La Niña like).

increase of rainfall (+8%) and cloud fraction (+4%) but a marked increase of air temperature by +3°C relative to the average of 1980-1999 is expected (Meehl et al. 2007). The decadal increase of +0.3°C is higher than the observed trends of the recent past (+0.22°C NCEP/NCAR; +0.14°C at Loja, see above). Nevertheless, data as well as model calculations point to a clear warming trend in the study area. Ecological importance of such a thermal shift is obvious. By assuming a stationary average lapse rate of –0.61°C per 100 m of elevation increase (Bendix et al. 2008a) until 2100, the increase of temperature must result in an altitudinal shift of ecothermal belts in the study area (Fig. 6). As a consequence of a temperature increase by 3°C in the course of the 21st century the area with an average air temperature equal or higher than that of the ECSF meteorological station today (1860 m a.s.l.; 15.5°C) would increase by a factor of 4.4 and the current thermal conditions of the ECSF met station would shift from 1860 to 2300 m a.s.l.

This must effect changes in ecosystem functional components and processes, e.g. the soil respiration rate and in turn the carbon balance and deposition of organic material. Iost et al. (2008) showed that soil carbon efflux is highly correlated to soil temperature and moisture, with flux rates of around 9.32 Mg C ha^{-1} a^{-1} at 1890 m asl (the elevation of the ECSF met station) and 3.83 Mg C ha^{-1} a^{-1} at around 3000 m. By assuming that soil temperature will linearly rise by ~3°C (concomitantly with a decrease of moisture), the thermal

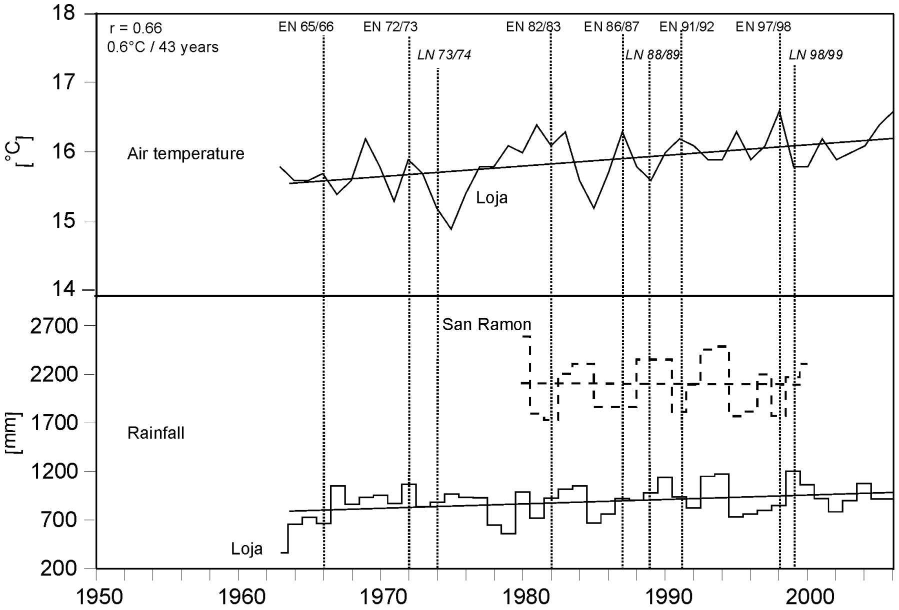

Fig. 5. Climate trends from observational data in the wider study area of southern Ecuador (data source: INAMHI(INAMHI: Instituto Nacional de Meteorología e Hidrología del Ecuador

area increase by 60% (Fig. 1) with high efflux rates could boost the carbon efflux by additional 12.6 t C a^{-1}.

5 Climate change and biodiversity in the RBSF

5.1 A case-study: Impact of Climate warming on an ectothermic faunal group

Not much is known about the impact of climate warming on the tropical lowland rain forests. In mountains, an uplift of the altitudinal ranges of species must be expected and has been shown for European high mountain regions (Walther et al. 2005). Due to this uplift a general increase in plant species richness has been observed in temperate mountains (Klanderud and Birks 2003) but at the same time high altitudinal species which, because of the limited orographic height, can not escape to higher regions will go extinct (Grabherr et al. 2001, Theurillat and Guisan 2001). However, the reactions of plant populations to a temperature increase are slow compared to e.g. ectothermic insect groups. Fast changes in altitudinal ranges, species numbers and biodiversity can be expected for such type of organisms like butterflies and moths, if they find appropriate host plants in the new altitudinal range.

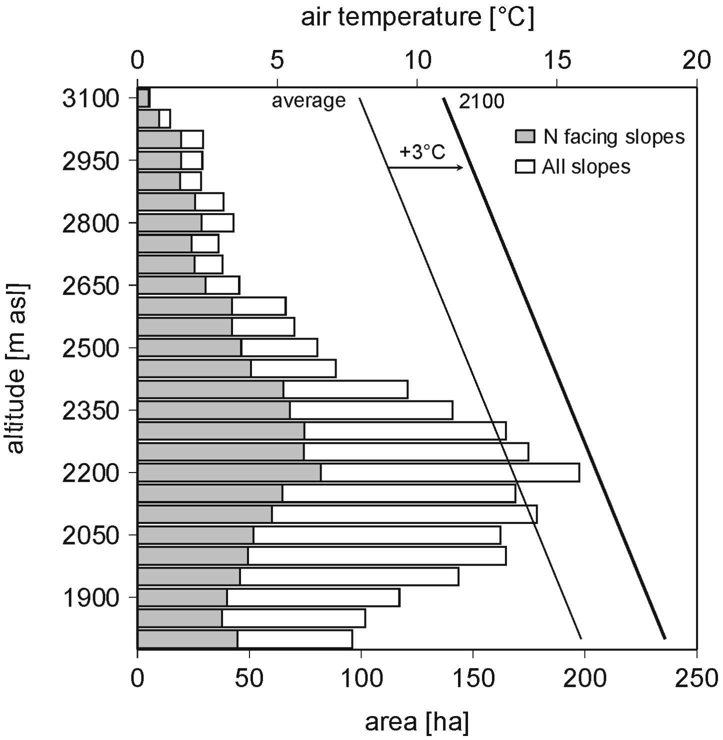

Fig. 6. Area of altitudinal belts of the study area (Fig. 1), average air temperature (1998 - 2006) and linear forward projection based on IPCC A1B scenario for 2100. Total bars represent the terrain height distribution respective of the entire area of figure 1, grey-shaded bars the area distribution of the north-facing slopes (south of the Rio San Francisco), which up to ˜2900 m are covered by natural forest. Note that the altitudinal distribution is displayed only for the landscape subset presented in figure 1, which implies that the centerpoint of altitudes is not in the lower but in lower-mid elevations (2,200 m a.s.l.)

In this regard, Chen et al. (2009) recently provided evidence from Mount Kinabalu in Borneo that 102 montane tropical moth species (Geometridae) have already extended their habitats by about 67 altitudinal meters over the past 42 years

The species-area approach: Colwell et al. (2008) could show for high neotropical mountains, that a temperature triggered upwards shift of species ranges is usually coupled with a reduction of the available space. One possible consequence could be that species which are more competitive (usually generalists) might cause the extinction of standing, less competitive species (most likely specialists) in the respective altitudinal belt. Of course, this simplistic approach should be refined by including interaction networks but especially in megadiverse regions like the study area, such data are very difficult to compile.

Nonetheless, , Thomas et al. (2004) applied a simple power law relation to estimate the proportion (E) of species in a region going extinct due to an altitudinal shift and range reduction as a result of climate change (species-area approach):

$$E = 1 - \left(\frac{\sum A_{new}}{\sum A_{original}} \right)^2 \qquad (1)$$

where A_{original} is the area initially occupied by a species and A_{new} is the future area projected for the same species.

To demonstrate a possible effect of climate change in the study area on ectothermic organisms, we exemplarily have applied the equation using published data of moths ensembles (,Tab. 11.3.1 in Fiedler et al. 2008), bearing in mind that moth species counts are almost necessarily incomplete (Brehm et al 2005). The calculation for the topographic situation of the north-facing slopes (Fig. 1) assumes that all species ranges will finally shift 500 m uphill to match their optimal thermal range upon the increase of air temperature by 3°C. Figure 7 reveals that species numbers may rise if the available area increases simultaneously with altitude, as indicated by the simulation for the altitudinal range areas up to 2200 m a.s.l. (Fig. 6). This situation implies that additional species are still present at lower altitudes, and that the natural forest as the basic resource remains intact in the target altitude. However, it should be kept in mind that the presented distribution of altitudinal range areas applies only to the study site and not to the entire eastern Cordillera. For elevations above 2200 m the species-area approach predicts losses of species as the available area decreases with altitude. According to the area distribution the number of moth species might decrease by ˜6% in the altitudinal range between 2000 and 2500 m, and by ˜68 % between 2200 and 2700m. If the suitable temperature range would shift from 2600 m to 3100 m, extinction of up to 92% of the species are predicted by the model. It should be stressed that the straightforward species-area model assumes that an increase of resources due to a warmer climate would necessarily end in an increase of species numbers, rather than of individual numbers of some of the respective species. This assumption is a serious constraint of the theory.

A comparison with current moths counts (Arctiidae, Geometridae, Pyraloidea combined) at different altitudes reveals that calculated species losses might be overestimated by the species-area approach. Fiedler et al. (2008) could show by light trap captures that the reduction of species number between 2180 and 2671 m a.s.l. in the ECSF forest ranges between 22% and 38% (depending on the selected location), in contrast to calculated -68% between 2200 and 2700 m a.s.l. by applying the area approach (Fig. 7). One reason of this overestimation could be that the species-area relation of individual moth groups differs (as e.g. the Geometridae, Brehm et al. 2003) resulting in changes of the quantitative composition patterns rather than in ultimate extinction.

Application of the energetic-equivalence rule: Regarding the prospected future temperature increase, the energetic-equivalence rule (Allen et al. 2002) in

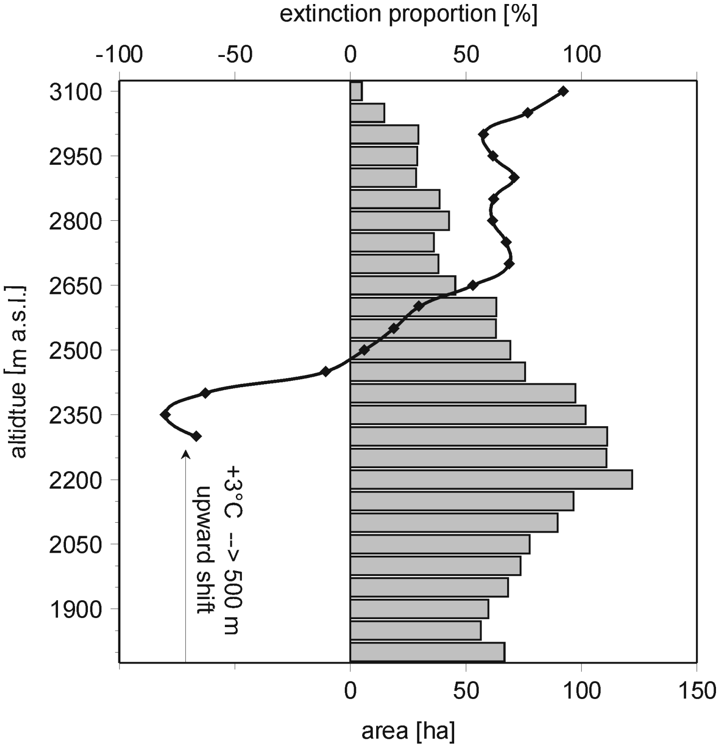

Fig. 7. Actual area of altitudinal belts for the north facing slopes of the study area (Fig. 1) and potential proportion of species going extinct based on the IPCC A1B scenario for 2100.

contrast to the species-area approach anticipates a general increase of species diversity, particularly along altitudinal gradients. The universal energetic relationship for ectothermic organisms is:

$$ln(S) = \left(\frac{-E}{1000 \cdot k}\right) \cdot \left(\frac{1000}{T}\right) + C_l \qquad (2)$$

where S is the number of species, E the activation energy of metabolism (= 0.78 V), k the Boltzmann constant (= 8.62 10^{-5} V K^{-1}), T the environmental temperature (K), and C_l is

$$C_l = ln\left[\left(\frac{B_0}{B_T}\right) \cdot \left(\frac{J}{A}\right)\right] \qquad (3)$$

where A is the range area of the community, J the number of individuals, B_T the total energy flux of a population (˜80 W km^{-2}) and B_0 is derived from the body size distribution.

$$B_0 = b_0 \cdot M^{\frac{3}{4}} \tag{4}$$

with $b_0 \sim 2.65 \cdot 10^{10}$ W $g^{-3/4}$ and

$$M^{\frac{3}{4}} = \frac{B_T}{xn \cdot b_0 \cdot x} \tag{5}$$

with xn is the population density (km^{-1}) and x is the Boltzman factor

$$x = e^{\frac{-E}{k \cdot T}} \tag{6}$$

To test the possible warming-induced effect on ectothermic individuals as predicted by the energetic-equivalence rule in the study area (Fig. 1) we exemplarily used published data on geometrid moths (Brehm et al 2005, refer to table 1 of this publication). It should be kept in mind that the samples are error-prone snapshot figures, most likely not representing the “real world”. Nevertheless, moths are by far the best investigated ectothermic organsimic group in the study area and thus, to date the only meaningful group to develop different climate change scenarios. The authors of the above mentioned study found 32,845 individuals (J in equation 3) and 1,075 species (S in equation 2) in the altitudinal range between 1800 and 2677 m a.s.l.. Restrictively it must be mentioned that parameter A in equation 3 is hitherto unknown due to a lack of sufficient observations in the surrounding area above and below the altitudinal range of 1800-2677 m a.s.l. Simplistically, A is assumed to correspond to the area of the respective altitudinal range as obtained from the digital elevation model (DEM) for the north-facing slopes (Fig. 1, A = 14.86 km^2). We further suppose that individual and species numbers are representative for this altitudinal segment, as we know that species numbers of Geometrids are fairly constant over this altitudinal range (Brehm et al. 2003, Fielder et al. 2008). For calculations of the population density we suggest that the light traps used by the authors are representative for an area of ˜50 by 50 m^2 (Brehm et al. 2005). Further, we apply a bulk approach where we consider the altitudinal range as a homogenous entity without any differentiation into altitudinal levels, which is characterized by the actual average annual air temperature of 13.1°C (based on meteorological data between 1998-2006). Finally the average air temperature shall increase stepwise by 1°C in the range of the expected future warming which is the parameter T in equations (2) and (6).

The prospected extent of warming depends on the chosen emission scenario, where a worst case scenario (SRES-A1Fl, see appendix) points to a maximum possible temperature increment of +6.4°C by the year 2100 while the most optimistic scenario family (B1, see appendix) predicts a change of +1.1°C (Solomon et al. 2007). Assuming a linear correlation between the average temperature of the investigated slope section and global warming rates according to the IPCC scenarios, Fig. 8 reveals that almost a doubling of species numbers could be expected for the altitudinal range of 1800-2677 m a.s.l.from the energetic point of view under the worst case warming rate.

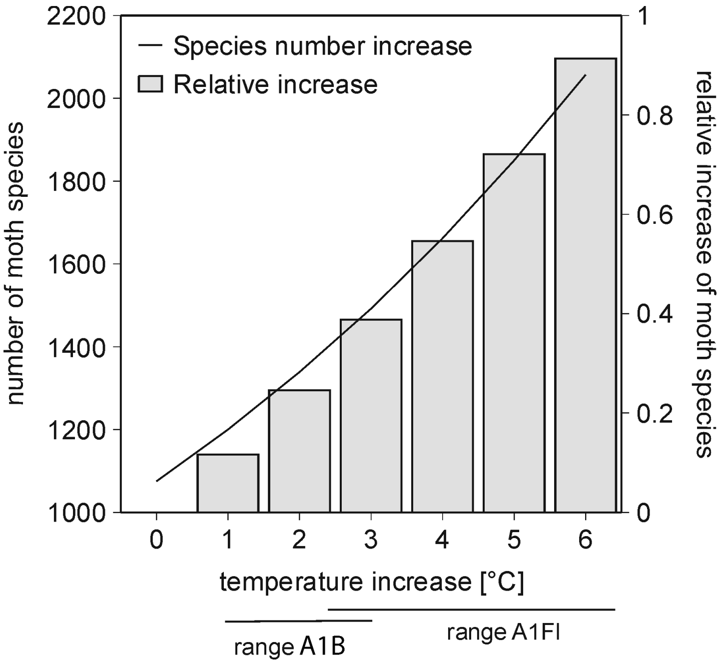

Fig. 8. Thermally induced increase of species numbers by 2100 for two different IPCC scenarios. (A1B represents a moderate and A1F1 the worst case scenario, see appendix). Relative increase is to the actual species number of 1075.

However, captures of Geometrid moths in lower altitudes under currently warmer temperatures do not reveal significant higher species numbers in contrast to the moth group of Pyraloideae (Fielder et al. 2008). These differences might be due to the snapshot character of the sampling, to effects of site selection and of the inhomogeneity of the area which might blur a potential effect of a warmer climate on species numbers. Furthermore, a species range uplift would need additional species from warmer altitudinal belts below. In this respect, immigration of novel species could be constrained by a limited local/regional species pool, preventing an increase of species even if warming would promote such a process.

Whereas the energetic-equivalence rule would generally allow for more ectothermic species at any altitudinal level, the species-area approach would at the same time diminish the number of species if a taxonomic group would be shifted upward to regions with decreasing area size.

It is obvious that communities of ectotherms have a specific altitudinal range to which they are thermally adapted. In Fig. 9 the results of the different approaches are shown for the geometrid moths, presuming a parallel and synchronous uplift of the lower and the upper boundary of an ectothermic faunal group upon warming without range extension. Note that the increase of species numbers predicted by the energy-equivalence rule upon warming is the same as given by the line in Fig. 8. The upper and lower boundary of the moth community after warming is calculated as follows:

$$\Delta hb = \frac{\Delta T}{|\Gamma|} \tag{7}$$

where Δhb is the altitudinal shift of the upper an lower boundary [m] at the temperature increase ΔT [°C] and the actual lapse rate Γ [°C m^{-1}]

The available area after warming is then derived by summing up the pixel area between the height boundaries in the digital elevation model (Fig. 1) for the north-facing slopes.

Regarding the species-area approach, species richness must decrease due to a continuous reduction of available area with increasing altitude, particularly at warming rates >3°C. By combining both approaches

$$S_{com} = S_{EER} - (1975 - S_{SAA}) \tag{8}$$

(where S_{com} is the species number of the combined approaches, S_{EER} of the energy-equivalence rule and S_{SAA} of the species-area approach) a clear reduction of species numbers (from 1,075 to 739 at +3.6°C = -31%) results for the most realistic range of warming (SRES A1B scenario with + 1.7 – 4.4°C by the year 2100). Under more unrealistic warming extremes, temperature-driven species number increase would somewhat overtop the area-driven species losses and consequently attenuate that losses.

The results of the case study highlight that the straightforward approaches commonly used to estimate global warming effects on species richness must necessarily imply a high degree of uncertainty irrespective of the ecosystem. First of all, the consideration of only one organismic group is unrealistic because altitudinal shifts are always embedded in complex interaction networks and thus, exact knowledge on the reactions of these networks due to global warming is required to properly estimate species extinction or altitudinal shifts of distribution patterns (e.g. Koh et al. 2004, Bascompte et al. 2006). It is obvious that this is a challenging task, particularly for the megadiverse mountain forest of southern Ecuador. Furthermore, human impact along altitudinal gradients can significantly blur the natural elevational gradient of species diversity (Nogués-Bravo et al. 2008) and thus, most likely mask global warming effects. Last but not least it must be stressed that model-required data even in the extensively investigated study area are still incomplete. Thus, intensive future research is necessary to refine the straightforward approaches tested in this section, and to provide sound knowledge for their application.

5.2 Climate change: Possible impacts on vegetation and plant diversity

Both the energetic-equivalence rule and the species-area approach are based on linear changes with altitude. However, in reality and especially on a lo-

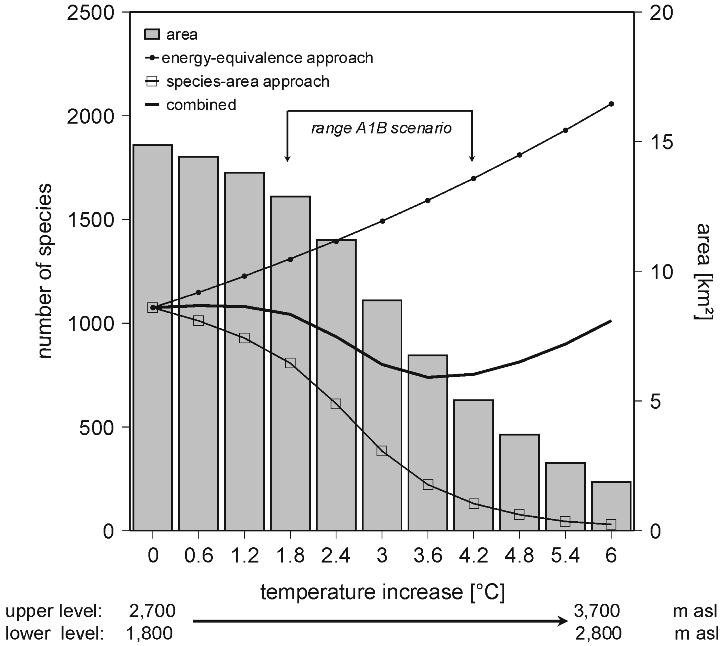

Fig. 9. Possible species losses or gains of geometrid moths on the North-facing slope of the RBSF forest (Fig. 1) under global warming conditions according to (a) the energetic-equivalence rule, (b) the species-area approach and (c) both approaches combined (equation 8). Note that the highest point in Fig. 1 is ˜3200 m a.s.l. so that the available area shrinks dramatically upon warming rates >2.4 °C.

cal scale non-linear ecological processes prevail, as evidenced by the frequent and small-scale changes of the vegetation. One of the non-linearities is the enormous plant species richness itself[6], each species being represented by relatively few individuals. The highly complex taxonomic multiplicity leads to a near-chaotic distribution of tree assemblages, where discrete vegetation zones are lacking giving rise to a huge continuous ecotone (Richter 2008). Contrasting to this continuous taxonomic turnover, extratropical plant assemblages form a comparatively clear system of characteristic, often monotonous altitudinal vegetation belts. While in the extratropical type of vegetation zonation, climate changes may trigger synchronous responses of more or less all components of a vegetation belt, in tropical mountain forests responses of individual species prevail, maintaining the heterogeneity, however with a changed species composition.

Asynchronous migration trends of plant species upon climate change must be assumed considering to the manifold biotic interactions, e.g. between plants and pollinators (e.g. Dziedzioch et al. 2003) or plants and mycorrhiza fungi

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[6] Probably also pertaining to insects

(Kottke et al. 2008). Clearly delimited local distribution patterns of some endemic taxonomically related species swarms indicate the importance of specific co-evolutionary traits. For example, a high degree of radiation is typical of many miniature orchid genera, of which Pleurothallidinae are prominent members in the RBSF forest. A possible factor for their frequently highly fragmented occurrence might be found in the presence or absence of appropriate mycorrhizal counterparts, as stated by Jost (2004) for similar features in the Rio Pastaza area further north. There is evidence that many of such highly specialised associations are highly fragile and easily dissociate when disposed to migration by substantial climate change. Since rates of range-shift are species-specific and because the members of interaction systems may react differently, niche-based models would be required to predict the effects of climate change on assemblages (Thuiller et al. 2005). Apart from the caveat discussed in the "Introduction" in tropical mountain rainforests of outstanding biological diversity such task appears illusive.

Phenological shifts in plant and animal communities upon climate change are likely, too, as detailed in the chapter on landscape history. On a short-term time-scale flowering and fruiting of 12 tree species showed in spite of the area´s perhumid climate a high extent of inter- and intraspecific synchronisation following the quasi-periodic oscillations of precipitation and cloudiness (Bendix et al. 2006). In the drier inner regions of Loja and Vilcabamba seasonal changes in rainfall and perhaps minimum temperature are most likely *triggers which induce flowering (Stimm et al. 2008).* The precipitation patterns during the last decades suggest slightly increasing rates for Loja on the western escarpment of the Cordillera Real (Vuille et al. 2008), which agrees with the aforementioned A1B scenario outlook, whereas Zamora on the eastern part may receive slightly less rainfall (Fig. 5). This situation supports the assumption that weakened mid- and upper tropospheric easterlies and strengthened westerlies would cause longer and more dry events. Concurrent clear sky conditions on the eastern side of the Cordillera, by uninhibited nocturnal radiation emission could result in lower minimum temperatures which sporadically might affect flowering and seed production and thus impair propagation. A slight trend towards more droughts is already visible, as only 8 rainless phases for over five days occurred between 1999-2003, while 21 such events were counted between 2004-2008.

Two extreme events of 16 and 18 consecutive days without precipitation in Nov. 2000 and 2005, respectively, resulted in severe desiccation damages and even complete withering of trees and shrubs. Ericaceous species suffered most in the timberline ecotone and the adjacent subpáramos, which is the uppermost vegetation belt, where mountain-top extinction of taxa could occur. All of the peaking nunatakker of the mountain consist of rocky cliffs and thus, species escaping upslope encounter increasingly unfavourable habitats (see "species-area approach", chapter 5.1). Consequently, climate warming would imply that drought sensitive species of an impressively endemic-rich altitudinal belt (Keating 2008) would have "nowhere to go".

The reason for a hampered immigration of montane forest species into the subpáramo is the stable position of the upper tree line of the cloud forest which consists of completely different plant communities. The tree line is located between 2800 and 3530 m a.s.l. (Fig. 10). While on a global scale mean soil temperatures (-10 cm depth) of 6.7 ± 0.8°C during the seasons of plant growth are considered the main reason for limiting growth of trees, Körner and Paulsen (2004) presented a lower value of around 5.5°C for the tropics, and Bendix and Rafiqpoor (2001) measured for even more elevated *Polylepis*-forests at Papallacta (in northern Ecuador) mean soil temperatures of 4.25°C. Environmental factors like abundant precipitation, air humidity and solar radiation can modify the impact of the temperature, and the local topography, soil conditions, natural disturbances and deforestation can add to this variation (Kessler et al. 2007).

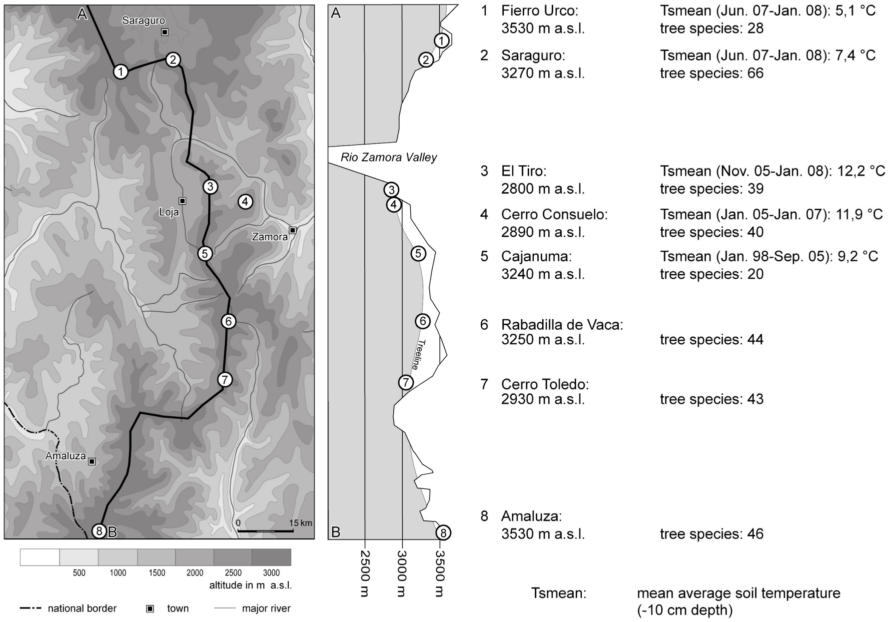

Fig. 10. Current position of upper tree line at the Ecuadorian part of the Andean Depression.

Soil temperature measurements from five different tree line sites around the RBSF area show that only the highest patches of forest approach the postulated temperature limit of +5.5°C (Fig. 10). In most cases soil temperatures are much higher and thus, are not considered a limiting factor for tree growth. Instead, the very strong and quasi-permanent easterly winds prevent development of tree crowns and as a consequence the uplift of the tree line.

Furthermore extremely high annual precipitation of up to more than 6000 mm/a (Emck 2007) cause water logging of the soils and leaching of nutrients and thus contributes to the inhibition of tree growth. Another point is the sporadically high global irradiance that by photodamage of the seedlings hinders tree regeneration and thus upslope extension of the forest (Baader et al. 2007). Finally, as in the majority of tropical mountains, livestock grazing and burning (Keating 1998) has a strong impact on the tree line. In summary only bushes and scrubs forming a species-rich subpáramo are encountered on the crests and upper slopes (Richter et al. 2008).

Given that temperature is not the limiting factor for tree growth above the upper tree line, warming fails as a reason for a future uplift of the current timberline. At the moment there are no indications for a forest encroachment into the subparámo. However, it should be kept in mind, that during early and mid Holocene the present-day subpáramo areas were covered by a forest-type vegetation (see chapter 3). An increase of the temperature would presumably allow tree species of lower regions to extend their ranges to higher altitudes thus enhancing tree diversity there. In the Andean Depression the upper tree line fluctuates between 2800 (El Tiro) and 3500 m a.s.l. (Fierro Urco in the north and Amaluza in the south (Fig. 10)). Different from the monotonous tree line in the high Andes the species composition of the tree line in the depression reflects the tree diversity of the upper mountain forest, which is usually an elfin forest. On the eight plots of 800 m^2 each (Fig. 10) between 28 and 66 tree species (DBH > 5 cm) were recorded, but a correlation between altitude and species number could not be detected. Given that the species patterns encountered at the eight sites represent tree diversity saturation situations other factors than thermal must be decisive in competition. Arrival of new species will result in enhanced competition putting more pressure on the recent timberline species, some of which might then completely disappear from the area.

Colwell et al. (2008) stated that suitable habitat corridors to higher areas are a precondition for an uplift of more thermophilous species. In the case of the eastern Cordillera of South Ecuador the numerous valleys from the precordilleran and Amazon forelands could represent such corridors. Many lowland rain forest species have outposts in western Amazonia (Miles et al. 2004) from where they could spread into the valleys and precordilleran ranges.

Another perspective of the effect of climate change on the vegetation leads to the idea that present plant assemblages may disintegrate because of asymmetric elevational range-shifts of the individual species (Williams et al. 2007). Asymmetric range-shifts can be due to species-specific reactions to changes of environmental factors which accompany the increase of temperature, e.g. the above mentioned dry spells. The logical consequence is not only the formation of novel species assemblages but due to the narrow ranges of many taxa also a more frequent formation of species gaps. An uplift of the condensation level as a consequence of warming (Still et al. 1999) implies an increased evapotranspiration especially in the cloud-rich elfin forest where evaporation is low. Species may not be able to adapt to drier conditions and because of the non-transgressibility of the tree line would be prone to extinction. Species-rich cloud and elfin forests with a high proportion of endemics might therefore suffer in particular from depletion, although they represent centers of speciation due to the high proportion of genetically plastic genera such as *Anthurium, Cavendishia* and *Miconia*.

Drought- and heat-tolerant species are most likely gaining terrain and upon reshuffling of communities input from anthropogenic habitats can play a significant role. Sources are pastures, abandoned former cultivated lands, roadside vegetation, and exotic tree plantations close to the RBSF and further downstream in the valley. Elements of these man-made habitats are powerful invaders of gaps in the mountain rainforest, where landslides and mud- or debris-flows form widespread entrance portals for newcomers. *Cortaderia jubata* and ferns like *Sticherus* spp. from roadsides, *Melinis minutiflora* from active and *Baccharis trinervis* and *Erica erecta* from abandoned pastures are examples of such invasive herbaceous and bushy plant species, all of which are light demanding. Therefore, they disappear upon canopy closure and usually can not gain a foothold in the dim subcanopy light climate of the natural forest. This situation is different from that in tropical lowland forests which are more prone to burning (e.g. East Borneo) and where fire is a natural trait of the ecosystem (Goldammer and Seibert 1989). However, several herbaceous road-side followers will benefit from climate warming and might invade the unshaded páramo, among them several highly competitive exotic grasses, such as *Poa annua*, *Dactylis glomerata*, or *Holcus lanatus.*

6 Conclusions

The question which meteorological element of a changing climate is the most important factor for a potential change of species ranges is difficult to answer even for a small mountainous area like the study site. From an energetic viewpoint, ectothermic organisms like moths or other arthropods could react to an increase of the air temperature by expanding their ranges uphill (Fiedler et al. 2008). Such reaction implies that the plants on which the caterpillars feed either already inhabit the enlarged area or that they expand their ranges in a comparable way as the insects, or that the herbivores are flexible in their diet. With respect to herbivorous insects no clear conclusion on the specificity of the insect – host plant binding has been elaborated so far (Stork 2007), but it is not unlikely in general that in an extremely diverse habitat like the study area, biotic interactions are commonly weaker, i.e. that organisms have several partners for the same kind of interaction. This is part of an insurance strategy as population sizes and densities of the species are usually low and the probability to find a specific partner in a short time slot is rather low. This also holds for other plant-animal interactions such as pollination or seed dispersal (Beck et al. 2008b). Nevertheless there are and will be thermal upper limits for ectothermic organisms as well as for some tree species (e.g. *Piptocoma discolor* and *Vismia tomentosa*) whose flowering and seed production suffered from a sequence of only a few consecutive cold days (Stimm et al. 2008). Such not very rare weather irregularities – spells of drought are another example – play a more crucial role in limiting the habitat of a sessile organism than the average temperature.

For tree species, irrespective of their thermal adaptation, the perpetual strong easterlies carrying extraordinary amounts of precipitation constitute another limitation of penetrating into today's subpáramo regions. This results in a significantly lower upper tree line than in other parts of the eastern Andean chains in central and northern Ecuador which are better sheltered against high wind speeds (Richter et al. 2008). At sheltered depressions even at El Tiro, small patches of a dwarf forest composed of species of the upper mountain or elfin forest survive which can be interpreted as outposts of the present or remnants of a former high mountain rain forest. Given a climate change to drier and less windy conditions these islets could be effective as nuclei for the natural reforestation of El Tiro's current subpáramo.

This perspective points to the findings of pollen analysis which revealed the occurrence of forest at the elevated sites of the area (El Tiro) during the most probably warmer and drier early-mid Holocene. Ongoing global warming could result in similar uplifting of upper habitat boundaries of tree populations, causing a stronger competition especially in the upper mountain forest region of the Andean Depression, as during early to mid Holocene. Some plant populations might become then very rare or locally extinct. Additionally, (and this might be even more serious) anthropogenic impact by fire in upper mountain regions strongly affects the subpáramo and upper mountain rainforest populations.

Warming, in general may be associated with changes in the atmospheric circulation. Future global warming simulations show for instance a poleward shift of the South Pacific and South Atlantic subtropical anticyclones, which generally cause alterations in the position and intensity of the tropical easterlies and the Walker-Circulation (Christensen et al. 2007). Similar changes in atmospheric circulation over South America were also suggested for the warmer period in mid Holocene by Grosjean and Nuñez (1994). The change in circulation is expected to weaken particularly the equatorial zonal wind over the Pacific (Vecchi et al. 2006). Polissar et al. (2006) stressed that a reduction of moisture transport from the Atlantic to the eastern tropical Andes in the Holocene is related to an increase of ocean temperature in the tropical eastern Pacific, a higher frequency of westerly winds and, as a consequence, the weakening of easterly stream flow to the tropical Andes.

An increasing frequency of drought events would be another consequence of such an altered circulation. Drought, as discussed in chapter 5.2, can substantially affect plant diversity patterns, in particular of the very sensitive timberline and subpáramo ecotones. Abundant tree line species with a high demand of moisture such as *Axinaea macrophylla*, *Hedyosmum racemosum* and *H. scabrum,* or *Weinmannia rollottii* may not be able to survive under such conditions and may be replaced by more drought tolerant species from lower elevations. Drought, in addition to its direct ecophysiological effects promotes the incidence of wildfires, as is also evident from the charcoal records from the mid and Late Holocene (see chapter 3). As it is known from tropical andine ecotones frequent fires can dramatically change species composition giving rise to a monotonous vegetation composed of species which can cope with the recurrent destruction of their aerial plant parts (e.g. Beck et al. 1986).

In that context questions arise concerning the emergence of “novel communities”. Identifiable and stable “communities” of coexisting populations (in the sense of the American “community ecology” approach) or “associations” (in the synsystematic sense) can hardly be found in the undisturbed mountain rainforests of southern Ecuador. These forests can be characterized by their structures rather than by the floristic composition. As mentioned above coexistence of organisms has more degrees of freedom which is one of the prerequisites of the high operative dynamics of these forests. As a consequence, newcomers with adequate environmental demands have a realistic chance to enter and integrate into the assemblage, the more so as dominant species are widely missing. While this concept of a “flexible community” seems to hold for the low- and mid-level mountain rainforests, the situation between elfin forests and páramos with their relatively clear boundaries rather corresponds to “fixed communities” which upon climate change could transform into “novel communities”.

7 Outlook

Thomas et al. (2004) predicted that species extinctions due to climate change will exceed those caused by direct human impacts like intensification of land-use and hence, claimed to re-evaluate conservation priorities. They argue that further measures to reduce the magnitude of anthropogenic climate change are now the major priority for conservationists. This way of priority ranking is dangerous because endeavours for conservation in particular of the tropical forests may suffer from redirecting resources (Lewis 2006) to technical solutions of the CO_2 problem. Rather, the activities to install a REDD-Regime[7] should be strongly supported in a country, which suffers the highest deforestation rate of the continent (Mosandl et al. 2008).

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[7] REDD: Reducing Emissions from Deforestation and forest Degradation<http://www.cbd.int/lifeweb/>

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Appendix: SRES-Scenarios

Future climate change is globally estimated by the ***I***ntergovernmental ***P***anel on ***C***limate ***C***hange (IPCC) with global circulation models. The basis of model runs is the radiative forcing due to alternating future greenhouse gas concentrations in the atmosphere. The concentrations are defined by socio-economic scenarios which are constructed with special reference to the production and evolution of greenhouse gases and aerosol precursor emissions during the 21st century. The scenarios are published in the third IPCC Assessment Report as a ***S***pecial ***R***eport on ***E***missions ***S***cenarios (SRES) and subdivided in four narrative storylines, labelled A1, A2, B1 and B2 (Nakicenovic and Swart 2000). The following scenarios/scenario families are addressed in the current chapter:

B1: This scenario family assumes a convergent world where global population peaks in mid-21 century and declines thereafter. With respect to greenhouse gas emissions it optimistically assumes rapid changes in economic structures toward a service and information economy, with significant reductions in material intensity, and the introduction of clean and ressource-efficient technologies.

A1: The future world in this scenario family is characterized by a very rapid economic growth (Business as Usual, most likely), global population that peaks in mid-century and declines thereafter, and rapid introduction of new and more efficient technologies. In contrary to B1, A1 is more prone to emissions where the A1B scenario is moderate by balancing across energy sources while the A1FI is fossil intensive, generating highest emission rates.

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