

Article

Vegetation Succession on Degraded Sites in the Pomacochas Basin (Amazonas, N Peru)—Ecological Options for Forest Restoration

Helge Walentowski ^{1,*} , Steffi Heinrichs ^{1,2}, Stefan Hohnwald ³, Alexander Wiegand ¹, Henry Heinen ¹, Martin Thren ¹, Oscar A. Gamarra Torres ⁴, Ana B. Sabogal ⁵ and Stefan Zerbe ⁶

¹ Faculty of Resource Management, HAWK University of Applied Sciences and Arts, Büsingenweg 1a, 37077 Göttingen, Germany; sheinri@gwdg.de (S.H.); Alex_Wiegand@gmx.net (A.W.); henry-heinen@web.de (H.H.); martin.thren@hawk.de (M.T.)

² Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, Büsingenweg 1, 37077 Göttingen, Germany

³ Centre of Biodiversity and Sustainable Land Use—CBL, Platz der Göttinger Sieben 5, 37073 Göttingen, Germany; shohnwa@gwdg.de

⁴ Instituto de Investigación para el Desarrollo Sustentable de Ceja de Selva, INDES-CES, Campus Universitario, Calle Universitaria N° 304, Chachapoyas, Amazonas 01001, Peru; ogamarra@indes-ces.edu.pe

⁵ Faculty of Liberal Arts and Humanities, Pontifical Catholic University of Peru—PUCP, Av. Universitaria 1801, San Miguel, Lima 32, Peru; asabogal@pucp.pe

⁶ Faculty of Science and Technology, Free University of Bozen-Bolzano, Piazza Università 5, 39100 Bolzano, Italy; Stefan.Zerbe@unibz.it

* Correspondence: Helge.Walentowski@hawk.de; Tel.: +49-551-5032-245

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Abstract: The Andes of northern Peru are still widely covered with forests, but increasingly suffer from habitat fragmentation. Subsequent soil degradation often leads to the abandonment of overused forests and pastures. Ecological knowledge on the restoration potential, e.g., on dependencies of soil conditions and altitude, is scarce. Therefore, we compared soil and vegetation patterns along nine transects within the upper Pomacochas Basin, which is an important biodiversity corridor along the Andes, between remaining forests, succession sites and pastures. Anthropogenic successional and disturbance levels, geological substrate, and altitude have the most important ecological impacts on vegetation and tree species composition. Species responded to sandstone versus calcareous substrates, but also to depths of the organic soil layer, and light conditions. The absence of organic layers under pastures contrasted with the accumulation of thick organic layers under forest cover. Vegetation composition at succession sites revealed certain starting points (herbal stage, bush stage, or secondary forest) for restoration that will determine the length of regeneration paths. Pre-forest patches of *Alchornea* sp. and *Parathesis* sp. may act as habitat stepping stones for expeditiously restoring biocorridors for wildlife. The key findings can contribute to the sustainable use and conservation of biodiversity in a fragile ecoregion.

Keywords: soil-plant relationships; biocorridors; yungas; secondary vegetation; fragmentation

1. Introduction

The Andean landscapes in general, but especially in the central “Amazonas” region in northern Peru, are characterized by land-use mosaics shaped by environmental factors and processes, as well as current and historical human influence [1–5]. Even though northern Peru is still widely covered with tropical mountain, cloud, and fog forests, locally also called “yungas” [6,7], which is a biodiversity hotspot with a high level of species endemism [8,9], these forests are increasingly threatened by habitat fragmentation [10].

The Andean eastern slope with its lower and upper mountain rainforests are still a quite continuous belt from Colombia, Ecuador through Peru up to the “Andean knee” in Bolivia, where they pass into the Bolivian-Tucuman forests. These yungas are not only important for ecosystem functions, and for the provision of ecosystem services for human welfare (water, wood, non-timber products, etc.), but also harbor one of the richest bird and plant biodiversity on earth [11]. Up to now, Peru was able to maintain an almost widely intact natural heritage with its natural forests representing the center of endemic flora and fauna and connecting forested land with its biodiversity across latitudes [9,12]. The Pomacochas region has an exceptional position, as it is located at the interface of two intact and already protected massifs, the Alto Mayo in the southeast of Pomacochas and the Colan Mountains in the northwest [13]. With the expansion of settlements and agriculture, however, this important biocorridor as a passage for population exchange is under threat and has already experienced severe land-use changes (Figure 1). The important “Pomacochas-Pedro Ruíz-Gate” now forms two dead ends for plant and animal species coming from closed forests of the northwest or southeast. In the Pomacochas basin, only small residual forest islands are left and species have to use the remaining vegetation along stonewalls, windbreaks, silvo-pastoral systems, and hedges as connecting corridors. These biocorridors, if well managed, might bridge faunal and floristic populations through the Pomacochas landscape and might play an important role for the protection of endemic and/or threatened large animal species. Intended flagship species for nature conservation and eco-tourism for the Pomacochas region are, for example, the Peruvian Night Monkey (*Aotus miconax*, Aotidae; [14]), the Yellow-tailed Woolly Monkey (*Oreonax flavicauda*, Atelidae; [15]), the Spectacled Bear (*Tremarctos ornatus*, Ursidae), the Cougar (*Puma concolor*, Felidae; [16]), and bird species, like the Marvellous Spatuletail (*Loddigesia mirabilis*, Trochilidae; [17]), the Long-whiskered Owlet (*Xenoglaux loweryi*, Strigidae), and the Andean Cock-of-the-Rock (*Rupicola peruviana*, Cotingidae).

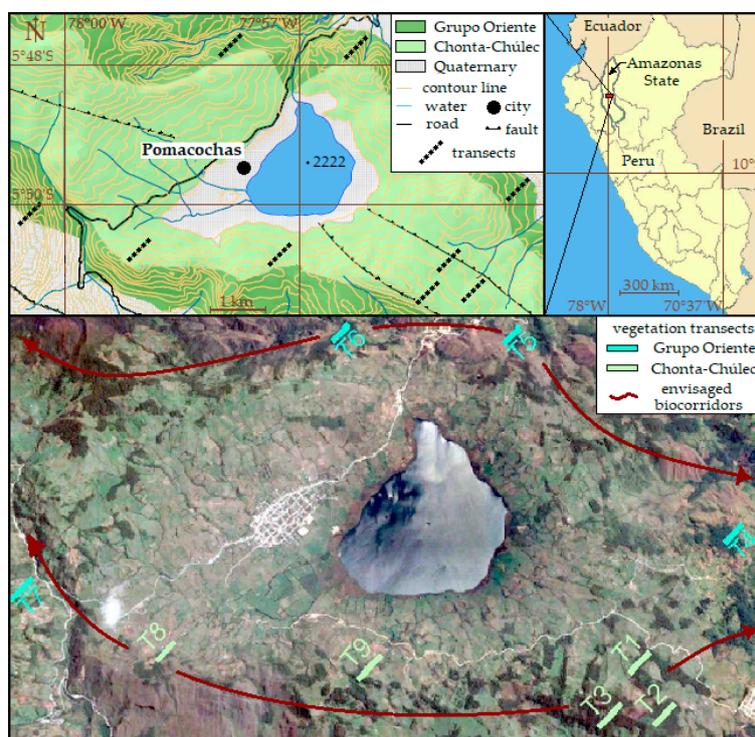


Figure 1. View on the Pomacochas study region in N-Peru and the locations of the soil/vegetation transects. Transects T1, T2, T3, T8, and T9 were established on the *Chonta-Chúlec* formation and transects T4, T5, T6, and T7 on the *Grupo Oriente* formation. On the satellite image (below, Google Earth pro, date 16 November 2016/19 August 2017), forest fragments can be identified by its dark green color that were partly integrated into the transects. Envisaged biocorridors for the local flora and fauna exchange are also indicated for future forest afforestation projects.

The ongoing establishment of pastures displaces the natural forest to more unproductive, marginal sites such as mountain tops and steep slopes by simultaneously producing abandoned land. On these abandoned sites, processes of vegetation dynamics occur depending on former land management, but presumably also on environmental factors, such as altitude, soil conditions, or geological substrate. Depending on these external factors, succession may successfully lead to the reestablishment of secondary forests representing an easy and cheap measure of passive restoration of biocorridors. It may on the other hand, also produce long-term and stable un-forested stages dominated by grasses, bracken-ferns, or shrubs [18,19]. In order to initiate active and effective restoration measures on such sites for re-establishing forest ecosystems with its functions and biodiversity it is necessary to gain knowledge on the fundamental interactions between vegetation, including tree regeneration and environmental preconditions.

Here, we investigated soil conditions and vegetation patterns in still existing, mainly fragmented, forests, and on abandoned land on the two dominant geological formations of the Pomacochas basin, i.e., the *Grupo Oriente* and the *Chonta/Chúlec* formation. They are characterized by contrasting geological substrates that are presumably affecting diversity and composition of the forest vegetation [20,21]. By identifying the impacts of former and current land use and geological substrate on soil conditions and on vegetation patterns, we aim to identify environmental conditions and assemblages of plant species that might indicate a high potential for successful forest restoration in such landscapes where timber and non-timber forest products support the local economies. Our three basic assumptions are:

- (1) anthropogenic successional and disturbance levels are crucial input variables for an effective restoration of biocorridors,
- (2) geological substrate is a strong driver for plant-site relationships and for habitat variety on the landscape level, and
- (3) intact mountain rainforests are strongly determined by intrinsic system-optimized water and nutrient cycles.

2. Materials and Methods

2.1. Study Area

The study region is the Pomacochas Basin in the State of Amazonas, N Peru. The Bongará Province in which the region is located is part of the Peruvian Inner-Andine Cordillera [22] within the northern central Andes and is characterized by mountain ridges with an altitude up to 3500 m a.s.l. that promote the existence of geological basins with respective lakes. They date back to the Andean orogenesis that started in the Cenozoic, which is an era with intensive erosion of the Eastern Cordillera causing significant sedimentation in the eastern sub-Andean cordillera with its characteristic landslides, faults, and basins [5,23]. The “Laguna Pomacochas” is the most prominent of these basins and is surrounded by the protected Alto Mayo, the Santuario Nacional Cordillera de Colán, and the Zona Reserva Río Neva mountain ridges. The Pomacochas basin is formed by four main geological substrates, i.e., (1) the uppermost geological deposits as quaternary colluvial soils, followed downhill by the Cretaceous (2) *Grupo Oriente* and (3) *Chonta/Chúlec* formations (Figure 1), and (4) the quaternary alluvial formation at the bottom of the basin. The *Grupo Oriente* formation consists of coastal and alluvial deposits and dates from a period between the lower and middle Cretaceous and is formed itself out of three layers: The inferior part is the Cushabatay formation, consisting of whitish-yellowish, sandstones, partially merged with silty claystone and grey siltstones. The medium part is the Esperanza formation and characterized by pelites and reddish-silty claystones while the superior part, the Agua Caliente formation, consists of greyish sandstones, which are merged with silty clay and siltstones. In contrast to that, the *Chonta/Chúlec* formation consists of fossiliferous limestone with small layers of grey and silty claystone. When compared with the *Chúlec* formation, the *Chonta* formation does not only consist of limestone, but also of sandstones, marl, and claystone, thereby relating more closely to the *Grupo Oriente* formation [22]. For both of the geological formations, the main soils are Umbrisols.

The region of the Pomacocha basin has been early settled by the Chachapoyas indigenous population (800 A.D.). From the 16th century onwards it was shaped by Spanish settlers. In the 1960s, notable exploitations of valuable Caoba timber (*Swietenia macrophylla* King) started by air transport from the former Florida Airport. This ecological and economical valuable species has almost completely disappeared until today. The construction of the National Road 5 in the 1970s facilitated further extraction of remaining valuable timber species. By the construction of this National Road, the latest immigration of settlers, especially from the origin of Cajamarca started. In 2005, the District of Florida/Pomacochas counted 5300 inhabitants. Most of them live from cattle breeding and milk production, especially for special fresh cheese products for local and regional markets. Because of lacking sustainability, considerable amounts of the landscape are abandoned former pastures or degraded forests that are now left for succession. These abandoned plots are covered with grasses, and bracken (*Pteridium arachnoideum* [Kaulf.] Maxon; Dennstaedtiaceae) or are subject to bush-encroachment as well as the establishment of secondary forest vegetation. However, until now, species composition is hardly studied in this region, but is important to assess the potential for natural recovery of these abandoned sites. So far, reforestation activities were mainly conducted for building wind shelter lines using the exotic species of the genus *Eucalyptus* and *Cupressus* or the native species *Alnus acuminata* Kunth (Betulaceae).

We investigated soil and vegetation in the Pomacochas basin with its characteristic lake (Laguna Pomacochas) in the centre of the basin at an altitude of 2071 m a.s.l. (77°57'W/5°48'S; Figure 1). The total area of the basin comprises 11,700 ha. Slopes reach up to 2559 m a.s.l. The climate of the region belongs to the Cold Humid Tropics with average annual temperatures of around 16–17 °C and an average annual rainfall around 1000 mm, which is usually interrupted by a dry season between September and December. Short-term climatological data by between 1970 and 1975 of the University of Chachapoyas (UNTRM) showed mean annual temperatures between 14.3 and 15.1 °C and a precipitation between 682 to 1092 mm at around 2200 m a.s.l. [5]. There might be an additional precipitation of 15–20% fog drip. The climate model of Climate data.org generates a current climate of 16.0 °C and 964 mm for Pomacochas at 2325 m a.s.l.

2.2. Soil Sampling

Nine transects of 400 m length were established in the transition zone of fragmented forest to agricultural land at the edges of the Pomacochas basin with development potential for a connective biocorridor (Figure 1). Three of the transects were located at the southeast of the lake Pomacochas in the rock formation *Chonta/Chúlec*. The transects four to six were arranged in the north of the lake where the *Grupo Oriente* formation was located and the last three transects were located in the southwest where soils of lime and quartzite exist. Soil profiles were regularly taken at five sampling points, separated by consecutive sampling intervals of 100 m along each transect. Each sample point was given a consecutive number beginning at the first knot from northeast moving towards southwest (Figure 2).

Sometimes it was not possible to expose soil profiles due to missing permits or inaccessible terrain. In total, 40 profiles were examined, 26 of them located on forest sites, seven profiles on abandoned (succession) sites, and seven profiles in pastures. 21 profiles were on substrate of the geological formation *Chonta/Chúlec*, 19 profiles were on the substrate *Grupo Oriente*. Forests (2071–2587 m a.s.l.; on average 2408 m) and succession sites (2128–2603; 2353) had a larger elevational range than pasture sites (2309–2453; 2381). For each profile, we identified and described the soil horizons and classified the soil type according to the World Reference base of Soil Resources (WRB) provided by the Working Group of the International Union of Soil Sciences (IUSS) [24]. Recorded topographic variables included slope aspect, slope inclination, and altitude in m a.s.l.

Additionally, 25 out of 40 soil samples were stored in polyethylene bags and were analyzed by the laboratory of the Universidad Nacional Toribio Rodríguez de Mendoza for physical and chemical soil properties. From six of the nine line transects, the soil texture was determined according to the physical

soil analysis by the Bouyoucos hydrometer method [25–28]. Soil-chemical research was focused on soil pH, plant available phosphorus (P_a), and exchangeable potassium (K_{ex}), measured in the organic layer, topsoil, and subsoil. They were selected as indicators for characteristic soil properties since (1) soil pH is considered a master variable in soils as it affects many chemical processes; (2) phosphorus is available to plants in limited quantities in most soils because it is released very slowly from insoluble phosphates and is rapidly fixed once again; and, (3) the potassium ion (K^+) is highly mobile and can aid in balancing the anion (negative) charges within the plant. Soil pH was measured by using a calibrated pH meter. As an estimate of plant-available phosphorus (P_a), the Olsen P method [29,30], which is based on extraction with 0.5 M sodium bicarbonate, was applied. Salt-exchangeable potassium (K_{ex}) was measured by an extraction of ammonium acetate in a spectrophotometer.

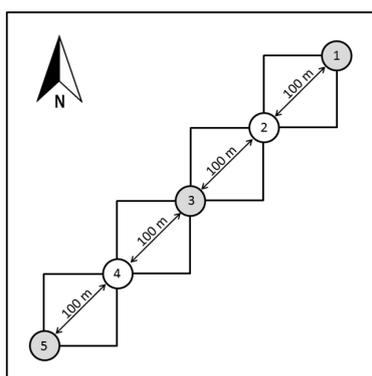


Figure 2. General set-up of a line transect containing five fixed sample points. Soil profiles were regularly taken at five sampling points, separated by consecutive sampling intervals of 100 m along each transect. Each sample point was given a consecutive number beginning at the first knot from northeast moving towards southwest. Vegetation data was sampled at three of the five sampling points along the soil transects, regularly at point 1, 3, and 5, i.e., separated by consecutive sampling intervals of 200 m along each transect.

2.3. Vegetation Sampling

Vegetation was sampled at three of the five sampling points along the soil transects, regularly at point 1, 3, and 5, i.e., separated by consecutive sampling intervals of 200 m along each transect (Figure 2). This approach ensured a precise spatial reference to the soil profiles and reduced autocorrelation by the doubled sampling interval. In line with the topic, vegetation sampling was focused on forests, and open to semi-open abandoned land. Grazed pastures and non-native tree plantations were accordingly excluded from the study. The clearly defined criteria of the stratified random sampling resulted in a set of 18 vegetation samples in forests (covered with trees and underbrush, characterized by shade-tolerant forest species), and six samples in open to semi-open succession sites, characterized by light demanding herbs and shrubs. Vegetation was surveyed in the tree (>5 m growth height), the shrub (1.5–5 m height), and the herb layer (<1.5 m height) by recording the cover of vegetation layers (directly estimated in%) and single species within the layers. For the herb layer, a 1 m² circle was used, for the shrub layer a 50 m² circle and for the tree layer a 500 m² circle. The maximum growth height for the tree layer was taken for each sampling point. Epiphytes, including mosses and lianas, orchids, and bromeliads on trees were not regarded in detail, as they are inappropriate to determine soil-plant relationships. Species were assigned to plant families and different growth forms according to the *Tropicos* data base of the Missouri Botanical Garden.

Data analysis focused on three aspects that might influence soil conditions and vegetation composition, i.e., (1) the effect of current and former land use, (2) the effect of geology, and (3) the effect of altitude. For the latter two aspects, we focused on forest plots as they represent both geological formations in sufficient numbers and were sampled along a 500 m elevational gradient. For comparisons

of soil and vegetation variables among land-use types and between geological formations, we used linear mixed effect models with transect as random factor (function `lme`, package `nlme`). Marginal (pseudo) R^2 values for fixed effects only were calculated using the `sem.model.fits` function (package `piecewiseSEM`). Pairwise differences were analysed with the Tukey-Test (function `glht`, package `multcomp`).

To discover the differences in vegetation composition between forest and succession sites as well as between the geological substrates in forests we calculated the percentage occurrence of different plant families per category. We further conducted non-metric multidimensional scaling (NMDS, `metaMDS` function, package `vegan` with Bray-Curtis-Distance on two dimensions) to investigate the compositional differences in the vegetation between land-use types and geological substrates. We calculated the standard error (95% confidence interval) for each category (`ordiellipse` function, `vegan` package). Altitude, soil, and vegetation variables, as well as cover values of individual plant species, were fitted to the ordination axes to evaluate their influence on species composition (function `envfit`, `vegan` package). We identified indicator species for forest and succession sites by performing an indicator species analysis according to Dufrêne and Legendre (1997) [31]. This analysis calculates an indicator value (IV) for each species per land-use type as the proportional abundance of a species within a group relative to the abundance in all of the groups multiplied by the proportional frequency of this species in each group (`indval` function, package `labdsv`). The calculated IV ranges between 0 (no indication) and 1 (perfect indication) with a perfect indicator being always and exclusively present in a certain land-use type. The significance of each indicator value is tested by Monte Carlo simulation using 1000 iterations [32]. To analyze the effect of altitude on soil and vegetation, we further conducted regression analyses with transect as random factor. In order to analyze the goodness of fit, the marginal R^2 was calculated.

All of the analyses were conducted using the R software version 3.4.2 [33] and the packages `nlme` (version 3.1-131; [34], `piecewiseSEM` (version 1.2.1; [35], `multcomp` (version 1.4-8; [36], `vegan` (version 2.4-6; [37], and `labdsv` (version 1.8-0; [38]. Statistical significance was assumed at $p < 0.05$ if not stated otherwise.

3. Results

The organic layer was significantly thicker under forests than under pastures and succession sites (Figure 3). Within forests, we found an increasing thickness of the organic layer along with the altitude (Figure 4). There were no further significant differences between the three main land-use treatments in all of the soil layers. Consistent across land-use types is the increasing soil-layer thickness with soil depth and a decrease in P_a and K_{ex} contents from upper to lower soil layers for forest and succession sites. A significant decrease from the organic layer to the top- and sub-soils could only be detected for the P_a under forests. The organic layer contained the highest concentrations of these macronutrients, but was completely missing at pasture sites. We further investigated if soil texture differed between land-use types as an indication if soil quality affected land management. Indeed, we found significantly higher proportions of sandy soils under forests and more clayey conditions under pastures (results not shown), while succession sites showed somehow soil conditions in-between the two extremes and were neither significantly different from forests nor pastures, respectively.

Table 1 gives an overview on how the vegetation structure and diversity reacts to the ecological differences of the land-use types, excluding the pasture sites. It shows that succession sites are significantly steeper than forested sites. Besides the fact that the tree cover was significantly higher in forests, shrub-layer cover and tree height were similar between the two land-use forms. There were some significant differences in plant diversity aspects, i.e., the number of plant families was much higher in forests than on succession sites. Also, the number of fern and tree species were higher in forests, while there were more grass species on the open succession sites. Regarded in proportions, grasses, herbs, and shrubs had a significantly higher share on species numbers on succession sites when compared to forests, while tree species had a higher share in species numbers in forests. The *Chonta/Chúlec* plots were located a little higher than the *Grupo Oriente* plots (cf. Table 3).

There were, however, almost no differences in vegetation structure and diversity between the substrates, with the exception of the shrub layer that was almost twice as dense on the *Chonta/Chúlec* plots. The most important plant families of forest and succession sites are shown in Figure 5. It elucidates that indicators of forest disturbance mainly belong to the families of grasses (Poaceae), composites (Asteraceae), roses (Rosaceae), and the members of the Oxalidaceae and Cunoniaceae. These families were much more frequent on succession sites, roses even exclusively on succession sites, and were found on half of all plots.

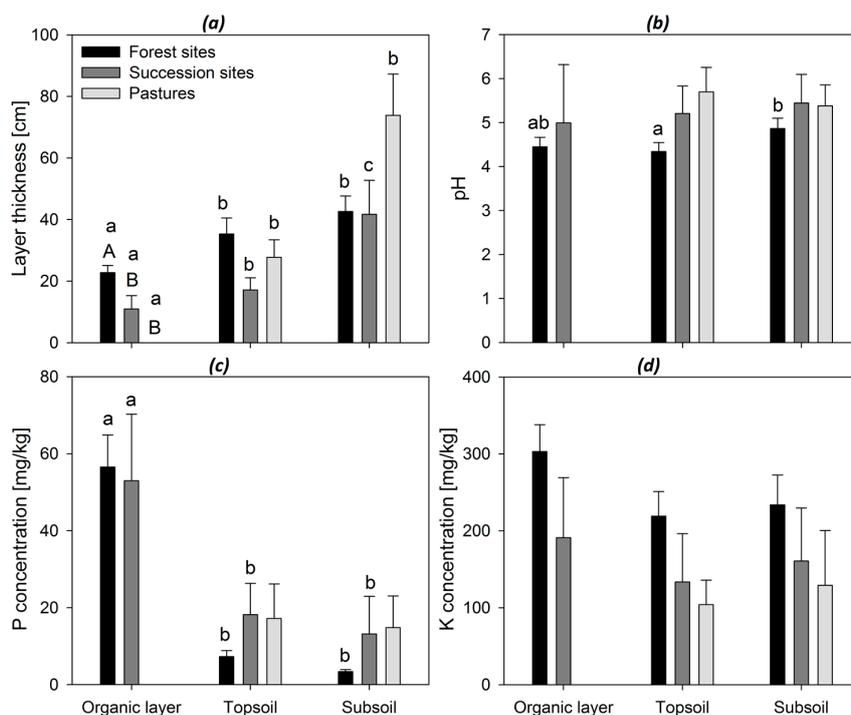


Figure 3. Effect of land use on (a) soil layer thickness, (b) pH_{H_2O} , (c) P_a , and (d) K_{ex} (with standard error) across three different soil layers. Upper case letters indicate significant differences between land-use types, lower case letters between soil layers (forest sites: $n = 26$, succession sites: $n = 7$, pastures: $n = 7$) based on linear mixed effect models with transect as random effect.

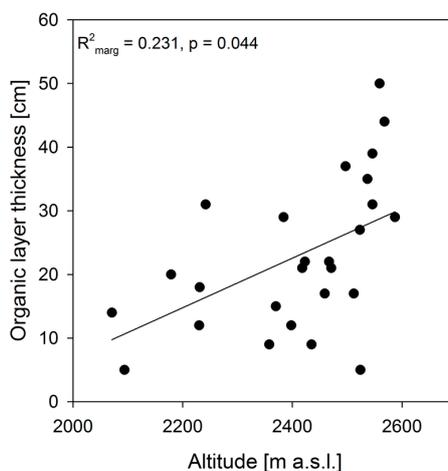


Figure 4. Relationship between altitude and organic layer thickness in forest plots. Given is the marginal coefficient of determination based on the fixed factor only and its p value as a result of the linear regression analysis with transect as random effect.

Table 1. Mean values (plus standard errors in brackets) of vegetation structure and species numbers (% = proportion) contrasted for the geological formations (only forest sites) and the two land-use types (forest and succession sites). Significant higher values at $p < 0.05$ are highlighted in bold based on linear mixed effect models with transect as random effect.

	<i>Chontal/Chúlec</i>	<i>Grupo Oriente</i>	Forest Sites	Succession Sites
	<i>n</i> = 10	<i>n</i> = 8	<i>n</i> = 18	<i>n</i> = 6
altitude [m a.s.l.]	2473 (18)	2293 (58)	2393 (34)	2311 (58)
slope [°]	14.4 (3.4)	18.1 (4.4)	16.1 (2.6)	29.4 (5.2)
vegetation structure				
cover tree layer [%]	78.5 (4.8)	80.0 (6.2)	79.2 (3.7)	16.7 (6.2)
cover shrub layer [%]	63.0 (8.4)	34.0 (6.2)	50.1 (6.3)	60.8 (51)
tree height [m]	27.2 (2.5)	23.8 (2.3)	25.7 (1.7)	19.6 (7.7)
vegetation diversity				
no. of plant families/plot	15.0 (0.9)	15.5 (1.9)	15.2 (0.9)	10.2 (1.4)
species number/plot	19.7 (1.9)	20.1 (2.3)	19.9 (1.4)	14.8 (2.1)
no. fern species/plot	1.4 (0.3)	1.4 (0.3)	1.4 (0.2)	0.5 (0.5)
no. grass species/plot	0.6 (0.2)	0.3 (0.2)	0.4 (0.1)	1.3 (0.4)
no. herb species/plot	1.7 (0.4)	1.5 (0.4)	1.6 (0.3)	2.2 (0.3)
no. shrub species/plot	2.9 (0.6)	2.0 (0.7)	2.5 (0.4)	4.0 (0.9)
no. tree species/plot	13.1 (1.4)	14.9 (1.1)	13.9 (0.9)	6.5 (1.8)
% ferns	7.5 (1.6)	7.0 (1.1)	7.3 (1.0)	4.6 (2.7)
% grasses	3.2 (1.1)	0.9 (0.6)	2.2 (0.7)	10.3 (2.9)
% herbs	9.1 (1.9)	6.6 (1.7)	8.0 (1.3)	14.9 (1.0)
% shrubs	14.0 (1.5)	8.4 (2.4)	11.6 (1.5)	28.1 (5.5)
% trees	66.2 (3.0)	76.5 (3.7)	70.8 (2.6)	40.3 (7.6)

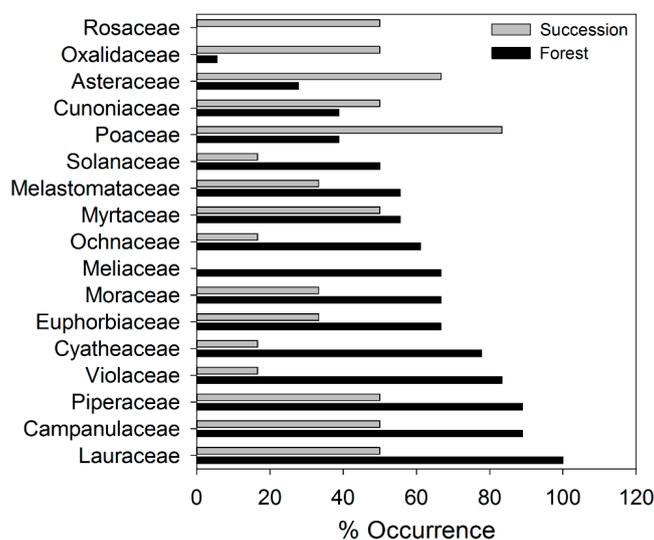


Figure 5. Percentage occurrence in plots of forest sites and succession sites. Shown are only families that occurred in at least 50% of the plots sampled in one of the two land-use types.

Most plant families had higher percentage occurrences in forests as compared to succession sites. Cyatheaceae and Violaceae occurred in more than 75%, Piperaceae, Campanulaceae, and Lauraceae, even in between 80–100% of the forest plots. However, Piperaceae, Campanulaceae, and Lauraceae also occurred in half of the succession sites, while representatives of the Meliaceae family solely occurred in forests.

The NMDS ordination of all the conducted vegetation samples (Figure 6) revealed patterns of species assemblages, suggesting a niche partitioning along successional gradients. The succession sites indicated a broad variance in their species compositions and several species partitioned their

niches. In contrast, the forest samples appeared as much more stable. According to the distribution patterns of species, the succession sites can be distinguished into three different stages, i.e., (1) a herbal stage which consists of bracken-fern (*P. arachnoideum*), Peruvian feathergrass (*Stipa* [= *Javara*] *ichu*), and the composite *Asplundianthus stuebelii* (Hieron.) R.M. King & H. Rob., (2) a bush stage, characterized by grasses (*Cortaderia* sp.), herbs (*Munnozia* sp.), and *Rubus* shrubs (Rosaceae) and *Baccharis* (Asteraceae), and (3) a pre-forest stage of shrubs to trees, which is mainly formed by the pioneer tree *Alchornea glandulosa* Poepp. (Euphorbiaceae), *Parathesis adenanthera* (Miq.) Hook. f. ex Mez (Myrsinaceae), and *Ophiocaryon* sp. (Sabiaceae). The (four) forests were mainly dominated by the tree species *Leonia glycyarpa* Ruiz & Pav. (Violaceae).

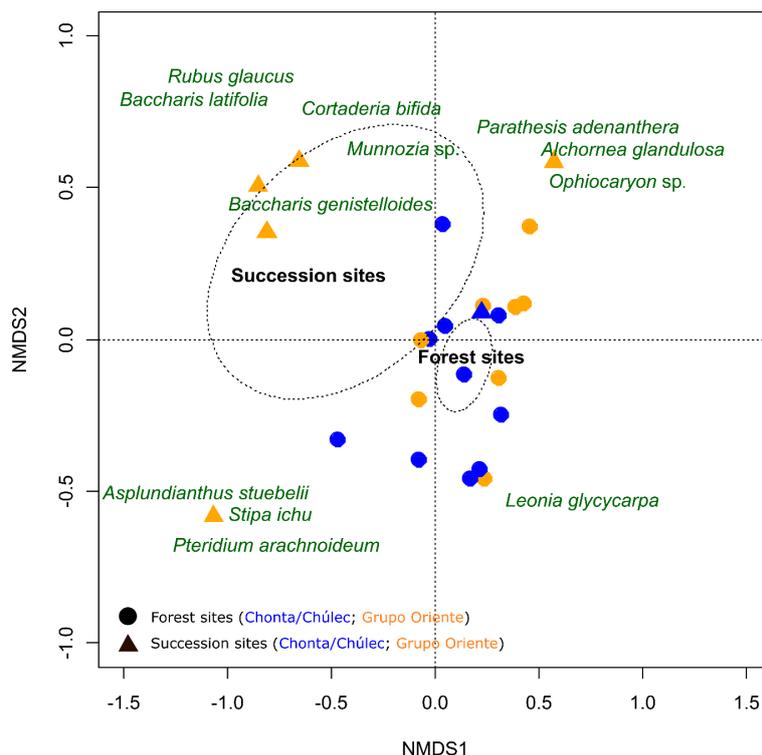


Figure 6. NMDS Ordination of all vegetation composition sampled in forest sites and succession sites. A bi-plot was created by correlating the plots scores of NMDS axis 1 and 2 with topographic, soil (organic layer and topsoil) and vegetation variables (no significance) and with cover values of individual plant species. Significantly correlated plant species are given in green color. Variables/plant species are shown if the correlation with the axis was significant ($p < 0.05$). The ellipses indicate the standard error around the centroids of the plots assigned to the different land-use types.

Indicator species analysis supported these results with the significant forest indicators *Leonia glycyarpa*, *Ocotea* sp., and *Cyathea* sp., while five species were identified as indicators for succession sites (*A. stuebelii*, *Baccharis latifolia* (Ruiz & Pav.) Pers., *Rubus glaucus* Benth., *Munnozia* sp., and *Oxalis medicaginea* Kunth) (Table 2).

Along the first axis of NMDS ordination of the forest plots, *Heliocarpus americanus* L. (Malvaceae) was associated with lowest scores (Figure 7). As this species was often recorded in tropical forest gaps, the first axis presumably represents a light gradient with the pioneer species *H. americanus* and the forest species *L. glycyarpa* representing both extremes. Along the second axis, low scores were associated with more sandy soils of *Grupo Oriente* (Table 3). The *Grupo Oriente* formation is characterized by *L. glycyarpa*, indicating a frugal, ubiquitous species, which is not limited by nutrient deficiency. In addition, we could identify *Hedyosmum racemosum* (Ruiz & Pav.) G. Don (Chloranthaceae) and the shrub/tree *Piper macrotrichum* C. DC. (Piperaceae) as significant indicators for *Grupo Oriente*

(Table 2), thus suggesting calcifuge species. The soils of the *Chonta/Chúlec* formation had slightly higher contents of clay, higher values of K_{ex} , and soil reaction when compared to the soils of *Grupo Oriente*, and derived from sites located at higher elevations (Table 3). The top of axis 2 was characterized by a sympatric *Piper* species (ecological vicarious to co-existing *P. macrotrichum*), by a *Carica* species and by *A. grandiflora* (Figure 7). They appear as more basophilous species and might be limited by acidity (low pH) and scarcity of nutrients.

Table 2. Results of indicator species analyses for geology substrate and land-use types.

	Live Form	Geology			Land-Use Type		
			IV	<i>p</i>		IV	<i>p</i>
<i>Hedyosmum racemosum</i>	Tree	Grupo Oriente	0.61	0.036			
<i>Piper</i> cf. <i>macrotrichum</i>	shrub/tree	Grupo Oriente	0.57	0.037			
<i>Leonia glycyarpa</i>	Tree				forest	0.76	0.018
<i>Ocotea</i> sp.	Tree				forest	0.72	0.005
<i>Cyathea</i> sp.	tree fern				forest	0.71	0.013
<i>Asplundianthus stuebelii</i>	Shrub				succession	0.50	0.014
<i>Baccharis latifolia</i>	Shrub				succession	0.50	0.011
<i>Rubus glaucus</i>	Shrub				succession	0.50	0.019
<i>Munnozia</i> sp.	Herb				succession	0.50	0.012
<i>Oxalis medicaginea</i>	Herb				succession	0.49	0.035

Table 3. Mean values (standard error in brackets) of different topographic and soil variables sampled in the 26 forest plots. Values were compared using linear mixed effect models with transect as random effect. Given are the *p*-values of the comparison.

	Formations Chonta/Chúlec	Formation Grupo Oriente	<i>p</i> -value
N	16	10	
Altitude	2492 (14)	2276 (34)	0.215
Slope	13.7 (2.1)	18.2 (3.7)	0.265
Organic Layer			
O-layer thickness (cm)	25.8 (3.1)	17.8 (3.0)	0.130
P _{OL} (mg/kg)	63.9 (10.0)	40.4 (4.7)	0.297
K _{OL} (mg/kg)	354.6 (29.3)	228.8 (41.3)	0.137
pH _{Ol}	4.4 (0.3)	4.4 (0.1)	0.833
Topsoil			
% Sand _{topsoil}	53.7 (4.1)	69.3 (2.9)	0.182
% Silt _{topsoil}	17.1 (1.2)	14.6 (1.1)	0.526
% Clay _{topsoil}	29.3 (3.5)	16.1 (2.0)	0.126
P _{topsoil} (mg/kg)	5.3 (1.3)	10.2 (2.2)	0.300
K _{topsoil} (mg/kg)	273.3 (32.9)	137.9 (32.6)	0.058
pH _{topsoil}	4.5 (0.3)	4.1 (0.1)	0.713
Subsoil			
% Sand _{subsoil}	44.3 (2.9)	62.5 (1.8)	0.099
% Silt _{subsoil}	18.8 (1.8)	19.2 (1.9)	0.995
% Clay _{subsoil}	35.5 (3.5)	18.3 (1.2)	0.079
P _{subsoil} (mg/kg)	3.2 (0.5)	3.6 (0.6)	0.704
K _{subsoil} (mg/kg)	255.0 (39.0)	208.4 (43.7)	0.984
pH _{subsoil} (mg/kg)	5.1 (0.3)	4.5 (0.1)	0.590

The highest diversity of plant families per plot was found at an altitude of 2250 m. The same was true for the diversity of tree species per plot (Figure 8). With increasing altitude, family and tree species diversity decreased for both geological formations. This elevational range revealed a unimodal relationship of plant diversity with altitude with an increase up to 2250 m and a decrease with higher elevation. Furthermore, altitude showed a positive relationship with organic layer thickness of forest plots (Figure 4).

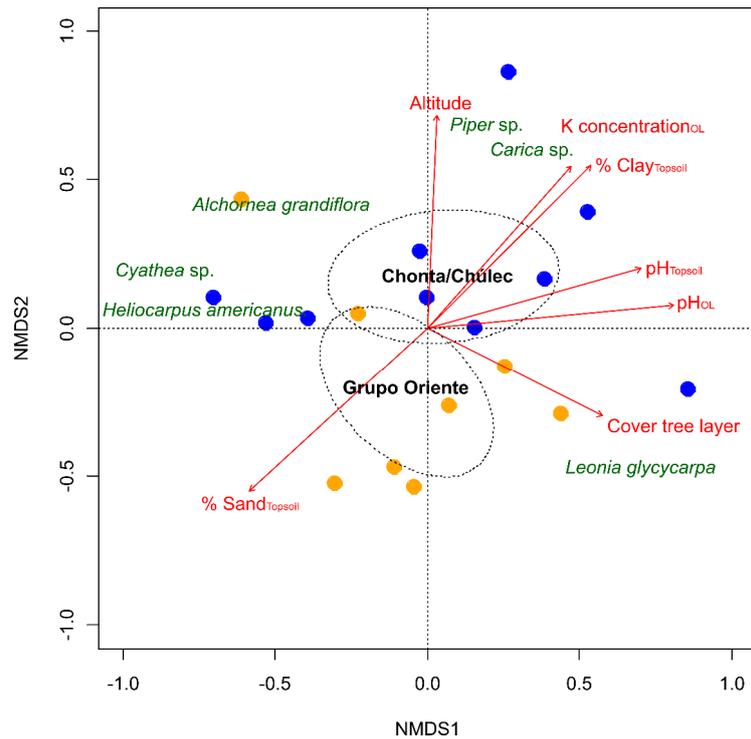


Figure 7. Non-metric multidimensional scaling (NMDS) Ordination of the vegetation composition sampled just in forest sites. A bi-plot was created by correlating the plots scores of NMDS axis 1 and 2 with topographic, soil (organic layer and topsoil) and vegetation variables (red arrows) and with cover values of individual plant species (displayed in green color). Variables/plant species are shown if the correlation with the axis was significant ($p < 0.05$). The ellipses indicate the standard error around the centroids of the plots assigned to the different geological formations.

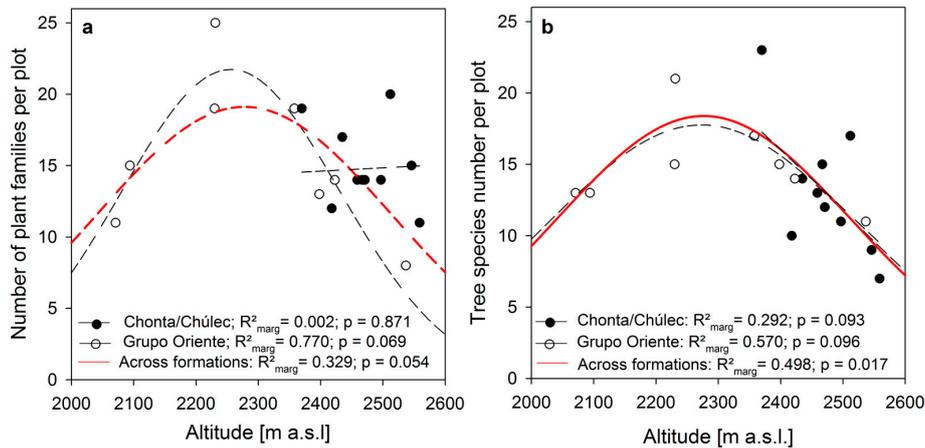


Figure 8. Effect of altitude on (a) the number of plant families and (b) the number of tree species per plot on forest sites. Best fit regressions were conducted separately for the two formations (black lines) as well as for all plots combined (red line) with transect as random effect. Quadratic functions best described the formation Grupo Oriente and all plots combined. Linear regressions were used for Chonta/Chúlec. Given are the marginal R^2 and the p -values of the regressions; dashed lines show non-significant results.

4. Discussion

4.1. Anthropogenic Successional and Disturbance Levels Are Crucial Input Variables for an Effective Restoration of Biocorridors

Our results show that the Pomacochas basin is characterized by a mosaic of different vegetation types as a result of different anthropogenic successional and disturbance levels and a small-scale heterogeneity of the geological substrate [3]. We assume that the pasture lands were largely limited to the quaternary colluvial soils in the surroundings of the “Laguna Pomacochas” before the settlement of new immigrants from Cajamarca in the 1970s, possibly supplemented by some forest pasturing. From 1980 onwards, though, steeper mountainous slopes were also cleared, causing reduction and fragmentation of tropical mountain forests, topsoil erosion, and disruption of the fragile water balance such as precipitation, evaporation, infiltration, water storage, and runoff. This presumably caused serious damage and has to be taken into account when considering the measures for an intermediate to long-term recovery of ecological functions and phytodiversity of tropical mountain forests.

Our data suggests to differentiate between three intermediate stages of disturbance and the tropical mountain forest. However, the distinguished stages must not necessarily be interpreted as a consecutive chronological sequence, since successional trajectories are highly varied and are rarely deterministic [39]. The velocity of successional changes highly depends on the availability of seed trees and the natural or anthropogenic, respectively, disturbance regime. If the secondary vegetation is subject to recurrent fires, grazing, or other disturbances, deflected (‘retrogressive’) succession sets in leading to apparently permanent biotic climax. Recurrent fires widely fostered (1) bracken-dominated (*Pteridium arachnoideum*) successional stages and succession has a specific endpoint [39]. This frugal fern species is the most successful cryptogam species on earth and holds a pivotal role in succession [40,41]. It is the most successful post-fire land degradation indicator, which may quickly invade after large scale disturbance events, accompanied by some small-seeded ruderal species of Asteraceae. Its rhizomes survive the fire and may gradually establish extensive subterranean networks. A bracken-dominated stage may be a longtime-persistent sub-climax for decades by preventing new colonization by shrubs and trees. Moreover, the series of successional trajectories includes (2) bush stages, which are characterized by the encroachment of spiny, shrubby to clambering vines, and scattered small shrubs that are 2–4 m high. Characteristic plants are Andean Raspberry (*Rubus glaucus* (Rosaceae), known locally as shirapoco, and *Baccharis latifolia* (Asteraceae) commonly known as chilca. Shirapoco is often used as living fence for corral livestock and can also be found alongside roads and quarries. In the environments of such starting positions, the bush encroachment may already establish after five years of abandonment after grazing or other disturbances. A third intermediate stage towards woodland classified as (3) pre-forest stage, includes taller shrubs and pioneer trees 10–20 m high like *Alchornea glandulosa* Poepp. (Euphorbiaceae), *Parathesis adenanthera* (Miq.) Hook. f. ex Mez (Myrsinaceae), and *Ophiocaryon* sp. (Sabiaceae). Rapid growth of early colonizing trees (“pioneers”) can bring about canopy closure in only 10 years after abandonment. Early woody regeneration consists of new seedling recruitment from seed rain and the seedbank [42] as well as resprouts. If undisturbed by grazing, tree felling and frequent fires, this secondary vegetation is more or less slowly invaded by primary forest trees like *L. glycyarpa* and can eventually develop into a community similar to that, which originally occupied the site. Forest sites have been undisturbed for at least 50 years. The latter one was distinguished not only by its species composition but also by humus-rich forest soils and high availability of key plant nutrients (P_a , K_{ex}). However, they are not untouched, since the Chachapoyas indigenous population, later the Spanish settlers and most recently the colonists from Cajamarca caused impacts and pressures on natural forests over centuries.

The anthropogenic successional and disturbance levels, as well as post-disturbance ecological legacies, can be crucial input variables for an effective restoration of biocorridors [39]. For example, the lack of P_a might be a decisive limiting ecological factor for the establishment of more nutrient-demanding species like *A. grandiflora*, and species of *Piper* and *Carica*. Putatively, a successful

re-establishment of demanding, late-successional species requires long-term regeneration processes connected with either secondary succession [2] or preceding the planting of early-successional tree species e.g., [43–45]. However, the succession model should not be interpreted too schematically. It might even be promising to plant some frugal late-successional tree species, like *L. glycyarpa*, directly into bracken vegetation without necessity of full soil-humus regeneration [18]. A higher forest restoration potential was found for the recovering secondary forest stage with *A. glandulosa*. These sites presumably represent recently exploited forests that have still a higher similarity to forests than the herbal or bush stage, suggesting that an intermediate recovery of tropical mountain forests might be more easily accomplished here. They may act as habitat stepping stones for a rapid restoration of biocorridors.

4.2. Geology Is a Strong Driver for Plant-Site Relationships and for Habitat Variety on the Landscape Level

Our results show, on the one hand, that forest vegetation differs between geological substrates, even though we only found two significant indicator species for the formation *Grupo Oriente*, which are *H. racemosum* and *P. macrotrichum*. Thus, they might be considered as calcifuge species associated with Cushabatay sandstone developing acidic soils. Sandstone affinities of *P. macrotrichum* were already stated by Sánchez-Saenz (1997) [46]. Specific plant-site relationships have to be considered when identifying species for forest restoration. On the other hand, the ordination of forest plots also showed some generalist species in terms of geology that rather characterize a light gradient with light-demanding pioneer species (*H. americanus*) and shade-tolerant forest species (*L. glycyarpa*). Thus, some species can be used as pioneer species on degraded soils that ameliorate the soil for late-successional species, a trajectory that is also considered for forest restoration in other climate zones. Typical neotropical pioneer taxa such as *H. americanus*, *Piptocoma discolor* (Kunth) Pruski (Asteraceae), or *Cecropia* sp. (Cecropiaceae) are known to occur in gaps in lower tropical montane forests at 1950–2100 m in southern Ecuador.

4.3. Intact Mountain Rainforests Are Strongly Determined by Intrinsic System-Optimized Water and Nutrient Cycles

Intact mountain rainforests of the study area were characterized by dark-brown humus rich soils (mainly Umbrisols and occasional poorly-drained Histosols). Since they are susceptible to erosion, they were limited to a natural or near-natural forest cover. Our results also demonstrate that the Pomacochas basin is located on the border between the Lower Montane and the Upper Montane Cloud Forest. These two forest types are often not clearly defined from each other due to missing indicator species or clear ecological limits. However, the peak in the number of families and tree species at 2250 m a.s.l. in our data indicate such a limit in our study area. The unimodal distribution that is found for forest plots located on the *Grupo Oriente* formation might be caused by niche overlaps and interlinking of Lower Montane Forests and Upper Montane Cloud Forest species between 16–18 °C, and the failure of thermophilous LMF species at an annual isotherm of 16 °C [47]. With increasing altitude, organic layer thickness increased what might require certain adaptations of tree species for germination, establishment, and growth [48]. The results provide support to the studies in tropical mountain forests of Costa Rica [49] and Ecuador [50,51], and suggest that the humus accumulation effects an autonomous cycling of macronutrients, which is virtually “decoupled” from the mineral soil.

5. Conclusions

Inhabitants of the Pomacochas basin become increasingly aware of the importance of intact forests since water catchment is essential to the local agricultural activity. In the Andean range, these forests also serve to avoid erosion and landslides, which currently pose a serious threat to local people [36]. Agriculture and pastures are fundamental for their livelihood, showing the necessity of an integrative approach of nature protection and sustainable land use.

Recent alarming deforestation rates have already caused severe impacts and put a high pressure on remaining forests. This applies even more in the light of fragile ecosystem functioning that is provided by intact forest cover and outstanding and fragile biodiversity of the Pomacochas region. Different ecological interrelations have to be regarded for forests restoration and conservation. Tailor-made solutions that are appropriate, affordable, achievable, and cost-efficient have to consider the following quintessences:

1. The anthropogenic successional and disturbance levels affect pedogenesis and nutrient cycling. They have significant influence on the achievable forest development type, since woody species have different temporal niches (early successional to late successional stages).
2. Soil properties and their relationships with underlying geological substrates determine the achievable forest-development type, as there are different site-plant relationships (e.g., calcifuge species; frugal species or more demanding species).
3. Altitudinal niche shifts of plants along the gradients of declining temperature, increasing moisture, and increasing humus accumulation towards higher elevation have to be considered.
4. A decisive goal-orientation of forest restoration can affect afforestation activities. Species that are rare, endemic, and/or threatened, and thus have a high significance for nature conservation could be used as target species for suitable habitat structure and functions along the biocorridors and to guarantee an ecologically sustainable development of the Pomacochas region.

Ongoing uncertainties require the implementation of standardized methods of surveillance and monitoring to assess targets based on evidence [52]. Moreover, we recommend advanced research of forest dynamics and ecological forest site classification by indicator species, as has been worked out in detail, e.g., in Central Europe [53,54]. Both of the measures can provide proper foundations to assess the regeneration potential in forests after selective logging. Intact Umbrisols and Histosols under natural or near-natural forest cover are particularly vulnerable to land degradation and should be protected. Therefore, it is important to find silvicultural alternatives that consider tree protection and sustainable management, for instance, by the integration of secondary vegetation [55,56] or the use of silvo-pastoral systems [57].

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