Plant Community Structure and Conservation of a Northern Peru Sclerophyllous Forest

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ABSTRACT

The vegetation near El Bosque Petrificado Piedra Chamana, in the northern Peruvian Andes, is evergreen sclerophyllous forest with significant shrub, epiphyte, and mat components. Important/characteristic genera include *Dodonaea*, *Polylepis*, *Oreopanax*, *Oreocallis*, *Myrcianthes*, and the mat-forming orchid *Pleurothallis*. A vegetation survey including 12 transects and 240 plots in high- and low-grazed areas documented 96 plant species. Compared with low-grazed areas, high-grazed areas had significantly fewer tree species, more herbs, and higher density of individuals. Both grazing categories exhibited high connectedness (as seen in network metrics) and positive biotic associations (nestedness), suggesting facilitation of some species by others, but high-grazed areas showed greater indications of positive associations (as seen in the C-score and V-ratio). These positive biotic associations may relate to the harsh environment and the role of keystone taxa such as *Dodonaea viscosa*, canopy trees, and mat-forming elements in moderating conditions and promoting species establishment. Only in the low-grazed areas was there any indication of competitive interactions (negative C-score/ less than expected species-pair occurrence). The shift in sign of the C-score, from negative in low-grazed areas to positive in high-grazed areas, indicates a loss of competitive interactions as a factor influencing community structure where grazing pressure is higher. Conservation of the area's natural resources would be advanced by protection of areas where the vegetation structure is more intact, better controls on grazing animals, and identification of development alternatives that would reduce pressure on the area's unique vegetation.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp

ONE OF THE NATURAL WONDERS of the northern Andes of Peru is a petrified forest known as El Bosque Petrificado Piedra Chamana, located near the town of Sexi in central Cajamarca. The site preserves the remains of a forest that was buried 39 million years ago by a volcanic eruption and subsequent mud flows (Woodcock *et al.* 2009). In the course of ongoing studies of the fossils, we observed serious soil erosion at the site and what appeared to be accelerating degradation of the area's sclerophyllous forest/shrubland, caused by some combination of grazing and browsing by animals, wearing of trails by humans and animals, and extraction of timber and firewood. In the summer of 2005, we began an inventory of the vegetation at the site to obtain information that would be useful in managing the site and in conservation planning in the area more generally. The species list from the site and an analysis of floristic relationships can be found in Aragón *et al.* (2006). Here we present a more in-depth study of this plant association that addresses the question of whether grazing and related disturbances are associated with significant differences in biodiversity and community structure. Our approach involved assessing low- and high-grazed areas with respect to differences in biodiversity; floristic composition; relative proportion of herbs, trees, and shrubs; positive and negative biotic associations; and network properties of the plant community. We expected that (1) grazing would be associated with decreased biodiversity and changes in floristic composition and the relative occurrence of herbs, shrubs, and trees; (2) competition would be an important influence on community structure, given the high levels

of biodiversity, and would be lower in areas where grazing was more prevalent and diversity lower; (3) the vegetation would be characterized by nestedness and high connectivity; and (4) nestedness would be higher in the high-grazed areas because of selective grazing and the protection that trees and shrubs afford to other species whereas connectivity would be higher where the vegetation is more intact.

The areas lies within the Amotape-Huancabamba Biogeographic Zone, which extends from the Rio Jubones in Ecuador to the Rio Chamaya in Peru and is a low area along the Andean chain, with mountains extending to 3500 m and low passes at elevations of *ca* 2000 m. High biological diversity and high levels of endemism of both plants and animals in this part of the Andes have been linked to environmental heterogeneity, the overlap of southern and northern species, and the fragmented nature of the forests, occurring on isolated mountain ranges separated by dry interandean valleys (Dillon 1997; Young & Reynel 1997; Weigend 2002, 2004; Weigend *et al.* 2005).

The department of Cajamarca comprises the core of this biogeographic zone, which also includes parts of the Peruvian departments of Piura, Lambayeque, La Libertad, and Ancash. Cajamarca has 71 percent rural population and is among the poorest departments in Peru (in our study area, 97% of the population has at least one basic need unfilled and 22.2% of children suffer from chronic malnutrition; Instituto Nacional de Estadistica e Informática [INEI] 2000). Although the highlands of Cajamarca were and are highly populated, population density in the area near the town of Sexi appears to have been low until the early 1900s (INEI 2000), possibly owing to the marginality of the land and the relatively late

date of settlement. The town was officially founded in 1942 (INEI 2000), with the first settlements dating to the 1910s when land was purchased from a nearby hacienda. The early settlers engaged in the practice of rainfed agriculture and *arrieraje* (transportation of products, including timber, using mules and horses to and from the coast) and raised animals including cattle, donkeys, horses, sheep, goats, and pigs. Since *ca* 1950, increased integration into national markets leading to intensified cultivation of commercial crops and ranching, ill implemented land reform, economic policies favoring cheap food imports and favoring urban over rural areas, and natural disasters, including droughts, have impoverished farmers and forced many to migrate either to coastal cities or the Amazon Basin (Deere 1990).

METHODS

STUDY SITE.—The study site (Province of Santa Cruz, Department of Cajamarca) is in the middle-montane zone of the Cordillera Occidental (6°35′ S, 79°10′ W; 2400–2600 m asl; Fig. S1). This region of the Pacific slope supports a range of dry-climate vegetation types, including desert and *Prosopis* woodland in low-elevation areas and lowest mountain slopes, deciduous dry forest at somewhat higher elevations, and *Acacia* woodland at middle elevations (< 2100 m). Epiphytes are a component of the vegetation of even the driest mountain slopes where Pacific fog is an influence.

Near Sexi, at *ca* 2400 m, the vegetation is evergreen sclerophyllous forest or shrubland. Important or characteristic genera include *Dodonaea, Polylepis, Oreopanax, Oreocallis, Myrcianthes*, and the mat-forming orchid *Pleurothallis*. The presence of epiphytes and a mat layer, as well as the diversity of herbaceous taxa, are distinct differences from evergreen-sclerophyllous chaparral of temperate latitudes (Thrower *et al*. 1977). The vegetation appears to correspond to the 'dry cloud forest' of the west slope of the northern Peruvian Andes described by Cano and Valencia (1992). These forests have sclerophyllous-leaved trees with abundant epiphytes, occur at 2500–3200 m, and are naturally fragmented and subject to seasonal droughts. The floristic affinities of the relict forests of northwest Peru, and of dry cloud forest in particular, are not well known (Dillon *et al*. 1995, Pennington *et al*. 2004, Weigend *et al*. 2005). Comparisons with other published floras reveal that the sclerophyllous vegetation near Sexi has closer floristic relationships to dry montane associations than to the humid montane forests of the region (Aragón *et al*. 2006).

Although Valencia (1992) suggests that fog is an important factor explaining the occurrence of dry cloud forest, Ellenberg (1979), in a review of Andean vegetation types, describes sclerophyllous forest as occurring at the same elevations as non-sclerophyllous montane evergreen forest but in drier conditions. Sclerophylly also occurs in the tropics in tropical savannah vegetation, in the upper montane zone, and in the upper canopy of lowland tropical rain forest (Niinemets & Sack 2006, Ribeiro & Basset 2007). In our study area, factors contributing to sclerophylly may include high light levels, high winds, and the porous substrate and acidic soils associated with volcanic rocks of the Huambos Formation (Wilson 1985). It also seems likely, following from Valencia

(1992), that fog and fog drip are important in ameliorating conditions and allowing for the structurally and floristically diverse plant association occurring at the site.

The dominant landscape features occurring locally are the Sexi plateau, with its caldera-like basin, the higher mountains of the surrounding Cordillera Occidental, and the deep canyon of the Rio Chancay to the east and south. The town of Sexi is situated in the bottom of a basin, referred to here as a caldera although its exact genesis is not certain, which supported a wetland before being drained. Inside the caldera and on the flanks of the plateau and surrounding hills, the vegetation is relatively well developed. Elsewhere, *e.g.*, on the steep slopes facing east toward the Chancay River or on some lower, flatter slopes, the vegetation is drier in aspect with sparse, low shrubs.

The immediate vicinity of the town of Sexi experiences extremely strong winds for several months of the year, possibly related to a wind-funneling effect associated with easterly moving air masses crossing the mountains. Dryness may be intensified by adiabatic flow off higher ridges and a rain-shadow effect. Fog associated with the Pacific inversion is frequent. The region is also prone to severe drought. The climate dynamics and variation of rainfall with elevation in the Huancabamba Depression appear to differ from other regions of the Andes (Richter 2008). El Niño is also a source of climate variability. We have reports of increased rainfall in El Niño years, but this relationship may not hold in all years and El Niño is associated with dry conditions further south in the Central Andes (Orlove *et al*. 2005).

VEGETATION SAMPLING.—The area near our study site is dedicated to free-range ranching, with agriculture no longer practiced to any significant extent. The patchy nature of the vegetation as well as the high density of herbs (including grasses), shrubs, and small trees were important considerations in determining our sampling strategy and choice of plot size. We established transects at 12 locations within the caldera. Environmental parameters varied little among these locations; for example, most plots were within 95 m in elevation of one another. At each location, we established two 10-m-long transects oriented approximately parallel (depending on topography) within patches of relatively intact vegetation in areas where the effects of grazing were not evident. We used two short transects rather than one long one because of the small size of some patches. Equivalent parallel transects were established outside of these patches where the effects of grazing were more evident. We made these determinations based on the presence of a mat layer and dense vegetation including trees in the case of the low-grazed areas and presence of open spaces, foraging trails, or animal dung in the case of the high-grazed areas. Transects were divided into 1 × 1 m plots for a total of 20 plots in each location. In each plot we recorded the identity and number of individuals of woody species and percent cover of herbs and grasses. For certain analyses, we calculated the total number of individuals of herbaceous species by dividing total percent cover by the average cover per individual. Voucher specimens were collected and identified in the field or at the herbarium and are deposited at the Herbarium Trujillense of the University

Nacional de Trujillo. Plant nomenclature follows W3TROPICOS (Solomon 1999).

Our study was assisted by local residents, who have considerable knowledge of the flora and its many species of useful plants, as has been documented for northern Peru by Bussman and Sharon (2006). We obtained information from them about vegetation history and land-use practices and history that informed our interpretations and suggestions regarding conservation.

DATA ANALYSIS.—We compared the average species diversity of low- and high-grazed areas and density of individuals by grazing category and life-form using two-way ANOVA. Species richness was calculated using the nonparametric estimator Chao2 (Colwell 2005), which is relatively unbiased, precise, and accurate compared with other estimators (Walther & Moore 2005); we performed 100 runs without replacements in EStimateS, v. 7.05 (Colwell 2005). We used Detrended Correspondence Analysis (McCune and Mefford 1999, Palmer 2006) as another representation of the differences between high- and low-grazed plots. This analysis was done with PCORD 4.20 (McCune and Mefford 1999) using the default settings (axes rescaled with a threshold of 0 and number of segments 26). Environmental information was not included in the multivariate analysis since the plots were relatively close together and did not vary in elevation, aspect, etc., to any significant degree.

The other analyses carried out were based on a matrix of presence–absence data for the plots sampled. Each reveals distinct aspects of community structure. 'Nestedness' expresses the tendency of uncommon taxa to occur in species-rich sites and has been utilized in several studies of plant community structure (Lázaro et al. 2005, Tirado & Pugnaire 2005). We used 'matrix temperature' T, which estimates the degree of nestedness of a matrix and offers a simple way to compare different matrices (Atmar & Patterson 1993). Perfect nestedness occurs when all species pairs are proper subsets of the assemblages found in species-rich sites (Atmar & Patterson 1993, Wright et al. 1998). We calculated T and its statistical significance with the program 'Nestedness Temperature Calculator' (Atmar & Patterson 1995), using 1000 randomizations in a Monte Carlo simulation. To compare networks of different matrix size, we used relative nestedness as defined by Bascompte et al. (2003).

C-score and V-ratio have been used to study community structure and the response of communities to disturbance (Gotelli & Arnett 2000, Sanders et al. 2003, Arrington et al. 2005, Mouillot et al. 2005, Tirado & Pugnaire 2005). C-score quantifies the average number of 'checkerboard units' (where if species A is present, B is not and vice versa) for all possible species pairs. It is a measure of whether species-pair covariance is greater or less than expected, with negative co-occurrence an indicator of possible competitive exclusion. We used the SIM2 algorithm and the sequential swap for this calculation. V-ratio represents the variance in species richness across plots and is a way of looking at aggregation of taxa in some plots/patches (Gotelli & Arnett 2000). If there are constraints on the number of coexisting species, the variance in species richness among plots will be small relative to the null model. Values of this index > 1.0 indicate positive covariance between species pairs and a

community in which positive biotic associations may exist. Values < 1.0 indicate negative covariance and a community in which competition may be important. To calculate the V-ratio we used the SIM2 algorithm (fixed columns and equiprobable rows). For both C-score and V-ratio, a null model was constructed by 1000 iterations of the original matrix, with statistical significance obtained by comparing the values of the indices from these null models with those of the observed matrix; the P-value was obtained as the proportion of the values (from the 1000 randomizations) that were more extreme than the observed value in a two-tailed t-test (Gotelli & Arnett 2000). We calculated these indices using Ecosim7 software (Gotelli & Entsminger 2007).

Network analysis, although most familiar as a method of studying food webs and plant–pollinator relationships (Bascompte et al. 2003, Proulx et al. 2005, Olesen et al. 2007), can provide information about the way associations grow and their stability in response to perturbations. There are several examples of application of this type of analysis to the study of plant communities (Heymans et al. 2002, Lázaro et al. 2005, Fuller et al. 2008). In the case of plant communities, proximity in space is assumed to involve relationships (e.g., competition, facilitation, allelopathy) that can be represented by network analysis and analyzed in network terms. This analysis required transforming the 2-mode matrix (species vs. plots) into a 1-mode species matrix in which species (nodes) are joined by links representing co-occurrence in one or more plot. The links were unweighted, so that a link has a value of 0 if a species pair co-occurs nowhere and 1 if it co-occurs in at least one site. The number of links between node i and all other nodes in the network is the connectivity of i, denoted by k_i. A network is characterized by (1) the average connectivity k of all nodes; (2) the characteristic path length l, the number of links along the shortest path between two species, averaged over all species pairs; (3) the network diameter d, the average length of the shortest paths between any two nodes; and (4) the average clustering coefficient c, the likelihood that two nodes connected to a third node will be neighbors. Other network relations studied were the relationship between connectivity k and species frequency, the connectivity correlation (the relationship between connectivity of a node and the average connectivity of all neighboring nodes, which provides information about compartmentalization/modularity of the network), and the cumulative connectivity distribution (the fraction of all nodes with $\geq k$ links plotted against k; if the network is scale free, this distribution can be fit to a power law). These analyses were carried out using the software Pajek (Batagelj & Mrvar 1998).

RESULTS

VEGETATION SURVEY AND ANALYSIS.—We recorded 4158 individuals, with 96 species in total (49 herbs, 23 subshrubs, 11 shrubs, 13 trees). The total number of species was 69 in both the high- and low-grazed areas. Forty-two species were shared by both communities; 27 species occurred only in the high-grazed areas and 27 only in the low-grazed areas. Compared with low-grazed areas, high-grazed areas had fewer tree species and more herbaceous species (Table 1). Density data showed a similar pattern, with high-grazed

TABLE 1. *Average number of species and density of individuals per plot (1 SD in parentheses) for the two grazing categories for evergreen sclerophyllous forest in northern Peru. Results of the ANOVA are shown: ns, nonsignificant.*

	Average no. species (no. species/m^2), $N = 240$		Average density (no. individuals/m^2), $N = 240$	
	Low-grazed	High-grazed	Low-grazed	High-grazed
Trees	1.3 (1.2)	0.4 (0.6)***	2.1 (2.5)	0.6 (1.2)***
Subshrubs	1.4 (1.0)	1.8 (1.6) ns	2.8 (2.9)	3.9 (4.0) ns
Shrubs	1.7 (1.1)	1.5 (0.9) ns	3.7 (2.9)	3.6 (3.0) ns
Herbs	16.5 (15.2)	31.2 (29.2)***	2.3 (1.1)	3.0 (2.2)**
All	6.7 (2.0)	6.6 (2.9) ns	25.1 (15.6)	39.1 (28.6)***

**$P < 0.01$, ***$P < 0.001$.

areas having fewer trees and more herbs. Overall there was a higher density of plants in the high-grazed areas (Table 1).

Total species richness, as estimated by Chao2, did not differ between the high- and low-grazed plots (81.9 vs. 73.4). The species–area curve (Fig. 1), rescaled to show the species accumulation by individuals as suggested by Gotelli and Colwell (2001), showed slightly higher biodiversity in the high-grazed plots, which is probably related to the higher abundance of grass and herbs in the high-grazed areas.

In the Detrended Correspondence analysis, axes 1 and 2 accounted for 13.2 and 7.5 percent of the total variance (Fig. 2). Gradient length for axis 1 was 5.9. The separation between the high- and low-grazed plots provides some support for the grazing categories we established, while the degree of overlap shown indicates that the plots can also be seen to comprise a gradient. Several plots in one transect that failed to follow the pattern may represent misclassifications during the field classification.

In general all the sites were strongly nested, *i.e.*, had temperatures that were significantly lower than simulated random temperatures (Table 2). The high-grazed plots exhibited the highest value (relative nestedness of 40%). Significant values of the nestedness measure *T* occur when there is an association of uncommon with common species, suggesting the existence of positive biotic associations in which common or widespread species mediate the occurrence of less common species (Lázaro *et al.* 2005).

C-scores differed from chance in both grazing categories (Table 3). However, the high-grazed plots had fewer checkerboard units and low-grazed plots more checkerboard units than simulated, *i.e.*, species tended to co-occur more often than expected in high-grazed sites, an indication of positive biotic association and possible facilitation of some species by others, whereas in the low-grazed sites, species tended to co-occur less often than expected, indicating that competitive interactions may be important in determining occurrence and community structure. The V-ratio was significant only for the high-grazed plots (Table 2), a further indication of positive biotic associations/facilitation for this grazing category.

Network analysis did not reveal significant differences between the grazing categories. Species connectivity ranged from 3 to 55 in low-grazed plots and 3 to 65 in high-grazed plots, with many of the same taxa appearing as most highly connected (*Baccharis tricuneata*, *Dodonea viscosa*, *Festuca* sp., *Senecio* sp., *Cronquistianthus* sp., *Pleurothallis* sp.; Tables S1 and S2). The link density (proportion of realized links) was 33 percent in both cases. The diameter of the networks was 3, meaning that most species can be connected by 1 (29%) or 2 (69%) links (*i.e.*, short path length and high clustering coefficient). These networks can thus be characterized as having small-world properties (since any two nodes can be connected by
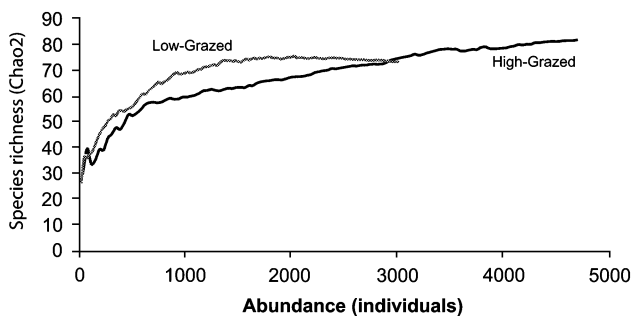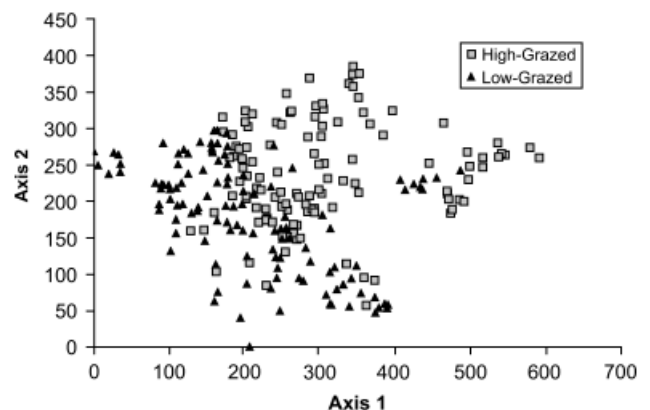

FIGURE 1. Estimated species diversity (Chao2) in the high- and low-grazed areas. The species–area curve has been rescaled to show the species accumulation by individuals.

FIGURE 2. Axes 1 and 2 from the Detrended Correspondence Analysis showing the two different grazing categories.

TABLE 2. *Analysis of nestedness N and relative nestedness N*(the association of uncommon with common species) for the two grazing categories. This measure is based on the matrix temperature T, with lower temperatures indicating a higher degree of nestedness. Significance is determined by comparing simulated matrix temperature T_{sim} with observed matrix temperature T_{obs}. Matrix temperature, comparison with simulated values, and nestedness values for two grazing categories (high and low). Fill, percentage fill; T_{obs}, observed matrix temperature; T_{sim}, simulated matrix temperature (average and standard deviation); P (Obs < Sim), probability that the matrix temperature is lower than observed; N, nestedness: $(100 - T_{obs})/100$; N*, relative nestedness: $(N - N_{sim})/N_{sim}$.*

	Fill (%)	T_{obs}	T_{sim} $(x \pm SD)$	$P_{(Obs < Sim)}$	N	N^*
Low-grazed	9.6	16.7	37.4 ± 1.4	< 0.001	0.833	0.33
High-grazed	9.6	12.4	37.3 ± 1.4	< 0.001	0.876	0.40

just a few links). Other network properties (negative connectivity correlation indicating some degree of modularity/compartmentalization [Fig. S2A]; positive correlation between connectivity and species frequency, showing that widespread species are most highly linked [Fig. S2B]; and a cumulative connectivity distribution that can be fitted to a truncated power law, indicating that most highly linked taxa grow prefentially [Fig. S2C]) are discussed in more detail in the Supporting Information (see also Appendix S1).

DISCUSSION

COMMUNITY STRUCTURE.—Although the grazing categories we set up provided a means of assessing differences in biodiversity and community structure associated with grazing, the existence of a gradient is also indicated by results of the correspondence analysis showing some overlap in the grazing categories (Fig. 2) and the occurrence of many species in both areas (Table S2). In addition, the network analysis showed that, although some highly linked taxa occur only in high- or low-grazed areas, other key taxa occur across the grazing categories.

The positive biotic associations indicated for both grazing categories, but which are stronger in high-grazed areas, could be

TABLE 3. *C-score ('checkerboarding' or negative species pair co-occurrence), V-ratio (variance in species richness across plots), and comparison with simulated values for the two grazing categories. Obs, observed values; Sim, simulated values (1000 runs); P, probability of observed values being significantly greater than (+) or less than (−) chance.*

	C-score			V-ratio		
	Obs	Sim	P	Obs	Sim	P
Low-grazed	79.9	78.2	0.002 (+)	0.88	1.00	ns
High-grazed	70.9	73.0	0.002 (−)	1.73	0.99	< 0.001 (+)

associated with a range of mutualistic relationships. Nestedness, for example, has been linked to pollination/seed dispersal systems involving synchronous flowering or fruiting (Lázaro *et al.* 2005). In our study area, however, we hypothesize that the positive biotic associations observed may relate at least in part to the harshness of the physical environment and biotic interactions that act to ameliorate it. In the low-grazed areas, tree species provide shelter and shade, a substrate for epiphytes, and promote fog drip and mat-forming taxa that are important in retention of soil and litter. In the high-grazed areas, the pioneering shrub *Dodonaea viscosa* acts to provide a more favorable substrate and microclimate, as well as protection from grazing, for the taxa growing around its base. Tirado and Pugnaire (2005), studying seven arid-climate vegetation types in Spain and Venezuela, found nestedness in two, including a Venezuelan sclerophyllous shrubland, where environmental conditions were the most severe. In a range of arid and semi-arid areas, researchers have been able to relate vegetation patchiness to positive feedback among species that meliorate conditions (generally by increasing availability of water and nutrients) and allow patches to arise or expand (Kefi *et al.* 2007, Scanlon *et al.* 2007, Armas *et al.* 2008).

The difference in sign of the C-score (Table 3), the most notable difference between low- and high-grazed areas and the clearest sign of the serious effects of grazing on the vegetation, is consistent with other studies in which negative co-occurrence (evidence of competition) in less-disturbed or later-successional associations is lost in the presence of disturbances such as introduction of aggressive alien species (Gotelli & Arnett 2000, Sanders *et al.* 2003, Arrington *et al.* 2005). Sanders *et al.* (2003) use the term 'community disassembly' to refer to the loss of competitive interactions as a factor influencing community structure.

The network analysis indicating tight linkages and high clustering of taxa (Table S2) and suggesting that tightly linked taxa grow preferentially (tend to have taxa added in their vicinity; Fig. S2C) is consistent with the idea that positive biotic associations are important in this plant community. This analysis also suggests a degree of modularity or compartmentalization in the network structure (Fig. S2B) and the existence of subnetworks that could increase community stability after disturbance or loss of highly linked taxa.

In terms of our initial expectations and hypotheses, we found that grazing is associated with changes in community composition but not necessarily species richness (at least at the disturbance levels analyzed and allowing for the increase in weedy herbs in the high-grazed plots). Competition, which was expected to characterize this plant community, was only apparent in low-grazed areas. As expected, these plants communities were nested and high-grazed areas displayed higher levels of nestedness. Our expectation that connectivity would be higher in low-grazed areas was not met as the network analysis failed to show significant differences between the grazing categories.

PHYSIOGNOMY AND DISTURBANCE.—Based on our results and information obtained regarding land-use history and disturbance factors, we can recognize three vegetation states that differ in physiognomy and can be related to different levels of disturbance (Fig. 3). The

UNDISTURBED FOREST

?

↓

INTACT SCLEROPHYLLOUS FOREST/SHRUBLAND

← tree canopy with epiphytes (bromeliads, orchids, ferns)

← shrub layer

← mat layer with Pleurothallis and other mat dwellers

↓

DEGRADED SHRUBLAND

erosion of substrate, breakup/loss of mat layer, loss of tree canopy and epiphytes
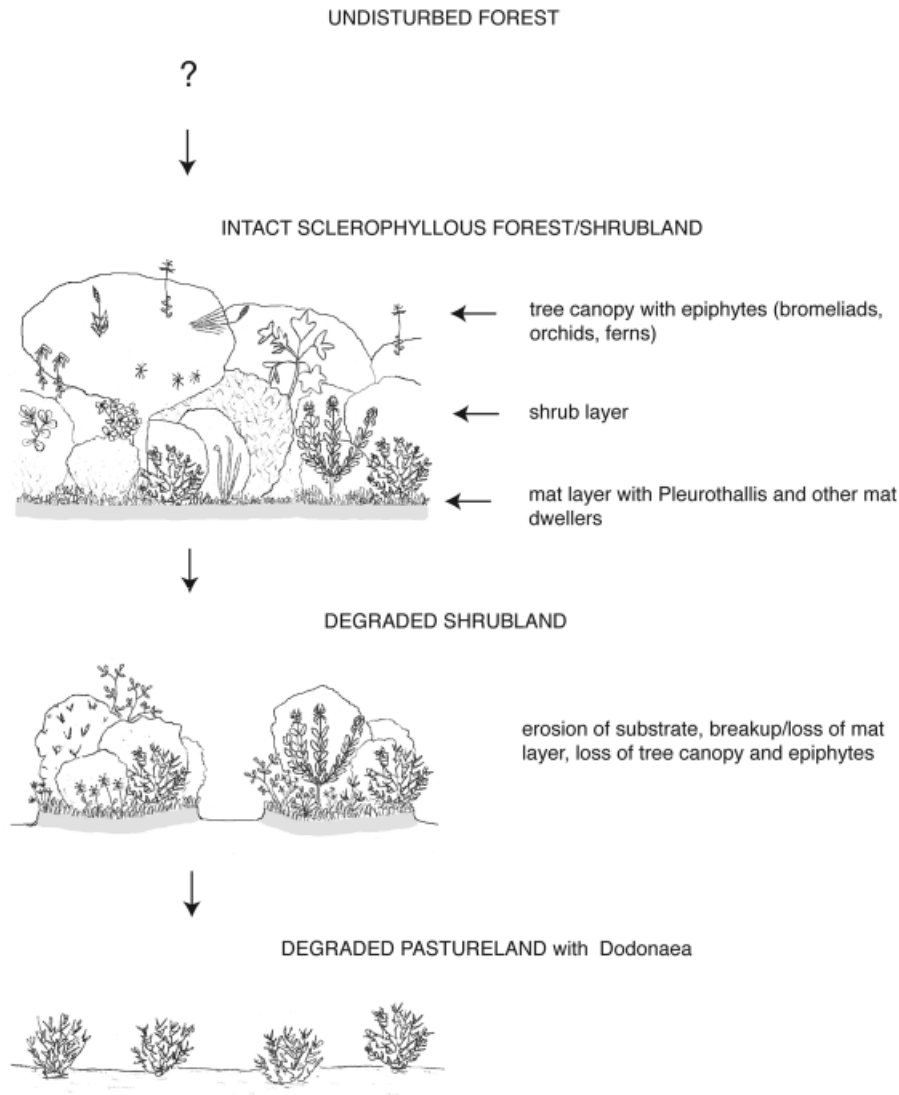
↓

DEGRADED PASTURELAND with Dodonaea

FIGURE 3. Physiognomic states of vegetation and hypothesized disturbance sequence, together with the corresponding changes in community structure.

study area is a mosaic of these different states, with states 2 and 3 more prevalent. As regards our sampling, our low-grazed plots correspond to state 1, whereas our high-grazed plots were in areas with characteristics of states 2 and 3.

In the first state, the vegetation cover is intact and trees up to 5–6 m in height either form a closed canopy or occur interspersed in the shrub layer. The taller elements of the vegetation support a diversity of epiphytes. A mat layer also occurs, made up of the ground-dwelling orchid *Pleurothallis* and other low-growing herbaceous and shrubby/suffrutescent taxa. Two aspects of the structure of intact vegetation appear to be particularly important. One is the presence of a mat that functions in retaining a litter and soil layer and providing a substrate for seedling germination and establishment. The other is the role of the canopy trees in facilitating fog drip that supplies moisture to tree roots and the lower vegetation layers; this phenomenon is well documented for humid montane forests (Bruijnzeel 2001) and may be even more important for drier-climate associations. This veg-

etation state may not be representative of undisturbed forest, which was probably taller, certainly more continuous than today's, and may also have differed floristically.

In state 2, the vegetation cover is discontinuous and isolated patches or islands of vegetation occur. Trees and their epiphytes are absent. Collection of firewood has its greatest effect on tree species, but grazing may as well. In an Argentina scrubland that shares some floristic elements with the vegetation at Sexi, livestock have a differential effect on the taller elements, including sclerophyllous leaved taxa often considered less palatable to animals. (Diaz *et al.* 2001). Wearing of trails has caused loss of the mat layer and the overlying vegetation cover, resulting in soil and organic matter being quickly lost through the porous substrate and an extremely degraded landscape in the areas between vegetated patches.

In state 3, the vegetation is a shrubland dominated by *D. viscosa*. A range of introduced species also occur, including herb and grass taxa that are not present where the mat is intact (Table S1).

The soil and litter layer is almost completely gone. The occurrence of *Dodonaea*, which has leaves that are unpalatable to animals, may relate partly to its ability to persist in the face of grazing/browsing and partly to its pioneering status and its seeds being eaten (and possibly also dispersed) by cattle.

CONSERVATION IMPLICATIONS.—A definitive assessment of the conservation status of the area's sclerophyllous vegetation would require a more extensive survey to establish the full extent of biodiversity and endemism and determine the spatial extent of this vegetation type and positive and negative interactions with people in the local community (McNeely & Scherr 2001). It would also be helpful to know more about plant–pollinator interactions, fruiting/flowering phenology, and other biotic factors that could underlie the facilitative/competitive relationships suggested by our analyses. Characteristics of the plants represented suggest that insects are the most important pollinators, and birds, and possibly mammals, the most important seed dispersers. The decrease or disappearance of certain groups of animals can have significant effects on the recruitment of plant species (Dirzo & Miranda 1990), although it is possible for agricultural landscapes to retain much of their biodiversity (Daily *et al.* 2003).

Factors contributing to the ecological fragility of the area include the severity of the dry season, the tendency toward drought, the porous and easily eroded substrate, the practice of free-range animal husbandry, and fluctuations in the numbers of grazing/browsing animals. Although the vegetation may have some degree of robustness in response to both natural and human-related disturbance (as seen in the facilitative relationships and aspects of the network structure), there still is a point at which fragmentation of populations will have serious consequences. This is especially true in the case of the tree species that are particularly important in community structure because of their role in moderating environmental conditions and facilitating the occurrence of other species and which may, in addition, have specialized dispersal or germination requirements. Whether populations persisting in small draws and inaccessible places will allow for recolonization is an important question, as is the degree to which natural successional processes are being altered owing to soil loss and erosion, decreased available moisture associated with lessened fog drip, and introduction of alien species.

Our results establish the biotic richness of this vegetation association, one of a diverse array of dry-tropical associations, mostly at low elevation, which are increasingly recognized as needing conservation efforts (Rodriguez & Young 2000). We are, however, unaware of any conservation initiatives or established reserves for montane sclerophyllous forests. Although the montane forests of nearby Cutervo National Park are unlike the vegetation at Sexi, there are similarities in socioeconomic context and the extent to which poverty may hinder the implementation of conservation measures. The mixed success of Cutervo (Peru's first national park) in conservation terms (Dillon 1997) may also show the limitations of strictly preservationist approaches that fail to take into consideration the needs of local populations. Until further studies can be done, we urge the adoption of measures aimed at protecting the vegetation cover, especially in areas where the tree canopy and epiphyte and mat components are more intact. Although our greatest concern is for tree populations, the epiphytic component may be especially slow to regenerate after disturbance (Gradstein 2008), and we suspect that reestablishment of the mat community may also be slow given the widespread loss of the soil layer. The creation of enclosures to protect remnant forest patches, identification of development alternatives that would reduce firewood collection and free-ranging ranching, and implementation of a sustainable development plan are measures that may help to save this unique vegetation.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Species with the highest connectivity (k) in high- and low-grazed areas.*
TABLE S2. *Network characteristics for the two grazing categories.*
FIGURE S1. Study area in Northern Peru.
FIGURE S2. Network analysis metrics: (A) Connectivity correlation for high- and low-grazed plots; (B) Relation between connectivity, k, of plant species and species frequency; (C) Cumulative distribution p $(\geq k)$ of the number of links k per plant species.
APPENDIX S1. Detailed description of network analysis.

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LITERATURE CITED

ARAGÓN, S., L. RIMARCHIN, J. AYASTA, AND D. WOODCOCK. 2006. Inventario preliminar de la Flora del Distrito de Sexi, Cajamarca. Arnoldoa 13: 358–367.

ARMAS, C., F. I. PUGNAIRE, AND S. E. SALA. 2008. Patch structure and dynamics and mechanisms of cyclical succession in a Patagonian steppe (Argentina). J. Arid Environ. 72: 1552–1561.

ARRINGTON, D. A., K. O. WINEMILLER, AND C. A. LAYMAN. 2005. Community assembly at the patch scale in a species rich tropical river. Oecologia 144: 157–167.

ATMAR, W., AND B. D. PATTERSON. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. Oecologia 96: 373–378.

ATMAR, W., AND B. D. PATTERSON. 1995. The nestedness temperature calculator: A visual basic program. AICS Res. University Park, NM and the Field Museum, Chicago, Illinois.

BASCOMPTE, J., P. JORDANO, AND C. J. MELIAN. 2003. The nested assembly of plant-animal mutualistic networks. Proc. Natl. Acad. Sci. U.S.A. 100: 9383–9387.

BATAGELJ, V., AND A. MRVAR. 1998. Pajek—program for large network analysis. Connections 21: 47–57. Available at http://vlado.fmf.uni-lj.si/pub/net works/pajek/.

BRUIJNZEEL, L. A. 2001. Hydrology of tropical montane cloud forests. Land Use Water Resour. Res. 1: 1.1–1.18.

BUSSMAN, R. W., AND D. SHARON. 2006. Traditional medicinal plant use in Northern Peru: Tracking two thousand years of healing culture. J. Ethnobiol. Ethnomed. doi: 10.1186/1746-4269-2-47.

CANO, A., AND N. VALENCIA. 1992. Composicion floristica de los bosques nublados secos de la vertiente occidental de los Andes Peruanos. Mem. Mus. Hist. Nat. UNMSM (Lima) 21: 171–180.

COLWELL, R. K. 2005. EstimateS: Statistical estimation of species richness and shared species from samples (Software and Users guide). Version 7.5.0. Available at http://viceroy.eeb.uconn.edu/estimates (accessed November 2007)

DAILY, G. C., G. CEBALLOS, J. PACHECO, G. SUZÁN, AND A. SANCHÉZ-AZOFEIFA. 2003. Countryside biogeography of Neotropical mammals: Conservation opportunities in agricultural landscapes of Costa Rica. Conserv. Biol. 17: 1814–1826.

DEERE, C. D. 1990. Household and class relations: Peasants and Landlords in Northern Peru. Duke University, Durham, North Carolina.

DIAZ, S., I. NOY-MEIR, AND M. CABIDO. 2001. Can grazing response of herbaceous plants be predited from simple vegetative traits? J. Appl. Ecol. 38: 497–508.

DILLON, M. O. 1997. Environments of the Andes: Montane forest. Available at http://www.sacha.org/envir/bosques/cutervo/cutervo.html (accessed September 2007)

DILLON, M. O., A. SAGÁSTEGUI, I. SANCHEZ, S. LLATAS, AND N. HENSOLD. 1995. Floristic inventory and biogeographic analysis of montane forest in Northwestern Peru. In S. P. Churchill, H. Balslev, E. Forero, and J. L. Luteyn (Eds.). Biodiversity and conservation of neotropical Montane forest, pp. 251–269. The New York Botanical Garden, Bronx, New York.

DIRZO, R., AND A. MIRANDA. 1990. Contemporary defaunation and forest structure, function and diversity—a sequel to John Terborgh. Conserv. Biol. 4: 444–447.

ELLENBERG, H. 1979. Man's influence on tropical mountain ecosystems in South America. J. Ecol. 67: 401–416.

FULLER, M. M., B. J. ENQUIST, AND A. WAGNER. 2008. Using network analysis of characterize forest structure. Nat. Resour. Model. 21: 225–247.

GOTELLI, N., AND R. K. COLWELL. 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4: 379–391.

GOTELLI, N. J., AND A. E. ARNETT. 2000. Biogeographic effects of red fire ant invasion. Ecol. Lett. 3: 257–261.

GOTELLI, N. J., AND G. L. ENTSMINGER. 2007. EcoSim: Null models software for ecology. Version 7. Acquired Intelligence Inc. & Kesey-Bear, Jericho, VT 05465. Available at http://www.garyentsminger.com/ecosim/ (accessed November–December 2007).

GRADSTEIN, S. R. 2008. Epiphytes of tropical montane forests—impact of deforestation and climate change. In S. R. Gradstein, J. Homeier, and D. Gansert (Eds.). Tropical mountain forests: Patterns and process in a biodiversity hotspot. Biodiversity and Ecology Series, Vol. 2, pp. 51–56.

Gottingen Centre for Biodiversity and Ecology, Gottingen, Germany.

HEYMANS, J. J., R. E. ULANOWICZ, AND C. BONDAVALLI. 2002. Network analysis of the south Florida Everglades graminoid marshes and comparison with nearby cypress ecosystems. Ecol. Model. 149: 5–23.

INSTITUTO NACIONAL DE ESTADISTICA E INFORMÁTICA (INEI). 2000. Banco de Información Distrital. Available at http://desa.inei.gob.pe/mapas/bid/ (accessed January 2006).

KEFI, S., M. RIETKERK, C. L. ALADOS, Y. PUEYO, V. P. PAPANSTASIS, A. ELAICH, AND P. C. DE RUITER. 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. Nature 449: 213–216.

LÁZARO, A., S. MARK, AND J. M. OLENSEN. 2005. Bird-made fruit orchards in northern Europe: Nestedness and network properties. Oikos 110: 321–329.

MCCUNE, B., AND M. J. MEFFORD. 1999. Multivariate analysis of ecological data, version 4.2. MJM software, Gleneden Beach, Oregon.

MCNEELY, J. A., AND S. J. SCHERR. 2001. Common ground, common future: How ecoagriculture can help feed the world and safe wild biodiversity. IUCN & Future Harvest, Geneva, Switzerland.

MOUILLOT, D., M. GEORGE-NASCIMENTO, AND R. POULIN. 2005. Richness, structure and functioning in metazoan parasite communities. Oikos 109: 447–460.

NIINEMETS, U., AND L. SACK. 2006. Structural determinants of leaf light-harvesting capacity and photosynthetic potentials. Prog. Bot. 67: 385–342.

OLESEN, J. M., J. BASCOMPTE, Y. L. DUPONT, AND P. JORDANO. 2007. The modularity of pollination networks. Proc. Natl. Acad. Sci. U.S.A. 104: 19891–19896.

ORLOVE, B. S., J. C. H. CHAING, AND M. A. CANE. 2005. Forecasting Andean rainfall and crop yield from the influence of El Niño on Pleides visibility. Nature 403: 68–71.

PALMER, M. 2006. Ordination methods—an overview. Available at http://ordi nation.okstate.edu/overview.htm (accessed December 2, 2008).

PENNINGTON, T. D., C. REYNEL, AND A. DAZA. 2004. Illustrated guide to the trees of Peru. David Hunt, Sherborne, UK.

PROULX, S. R., D. E. L. PROMISLOW, AND P. C. PHILLIPS. 2005. Network thinking in ecology and evolution. Trends Ecol. Evol. 20: 355–363.

RIBEIRO, P. S., AND Y. BASSET. 2007. Gall-forming and free-feeding herbivory along vertical gradients in a lowland tropical rainforest: The importance of leaf sclerophylly. Ecography 30: 663–672.

RICHTER, M. 2008. Tropical mountain forests—distribution and general pattern. In S. R. Gradstein, J. Homeier, and D. Gansert (Eds.). Tropical mountain forests: Patterns and process in a biodiversity hotspot. Biodiversity and ecology series, Vol. 2, pp. 7–24. Gottingen Centre for Biodiversity and Ecology, Gottingen, Germany.

RODRIGUEZ, L. O., AND K. R. YOUNG. 2000. Biological diversity of Perú: Determining priority areas for conservation. Ambio 26: 329–337.

SANDERS, N. J., N. J. GOTELLI, N. E. HELLER, AND D. M. GORDON. 2003. Community disassembly by an invasive species. Proc. Natl. Acad. Sci. U.S.A. 100: 2474–2477.

SCANLON, T. M., K. K. CAYLOR, S. A. LEVIN, AND I. RODRIGUEZ-ITURBE. 2007. Positive feedbacks promote power-law clustering of Kalahari vegetation. Nature 449: 209–211.

SOLOMON, J. 1999. Missouri Botanical Garden's VAST (Vascular Tropicos) nomenclature database. Available at http://www.tropicos.org/ (accessed December 2008).

THROWER, N. J. W., D. E. BRADBURY, AND H. L. DIAZ. 1977. Chile-California Mediterranean scrub atlas: A comparative analysis. Dowden, Hutchinson & Ross, Stroudsburg, Pennsylvania.

TIRADO, R., AND F. I. PUGNAIRE. 2005. Community structure and positive interactions in constraining environments. Oikos 111: 437–444.

VALENCIA, N. 1992. Los bosques nublados secos de la vertiente occidental de los Andes del Perú. Mem. Mus. Hist. Nat. UNMSM (Lima) 21: 155–170.

WALTHER, B. A., AND J. L. MOORE. 2005. The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators with a literature review of estimator performance. Ecography 28: 815–829.

WEIGEND, M. 2002. Observations on the biogeography of the Amotape-Huanc-abamba Zone in Northern Peru. *In* K. Young, U. Ulloa, J. L. Luteyn, and S. Knapp (Eds.). Plant Evolution and Endemism in Andean South America. *Bot. Rev.* 68: 38–54.

WEIGEND, M. 2004. Additional observations on the biogeography of the Amo-tape-Huancababa zone in Northern Perú: Defining the South-Eastern limits. Rev. Peru. Biol. 11: 127–134.

WEIGEND, M., E. F. RODRIGUEZ, AND C. ARANA. 2005. The relict forests of Northwest Peru and Southwest Ecuador. Rev. Peru. Biol. 12: 185–194.

WILSON, J. 1985. Geologia de los Cuadrangulos de Jayanca-Chepen. Bolletin no. 38, Serie A, Carta Geologica Nacional. Instituto Geologico Minero y Metalurgico, Lima, Peru.

WOODCOCK, D., H. MEYER, N. DUNBAR, W. MCINTOSH, I. PRADO, AND G. MORALES. 2009. Geologic and taphonomic context of El bosque Petrificado Piedra Chamana (Cajamarca, Peru). Geol. Soc. Am. Bull. 121: 1172–1178.

WRIGHT, D. H., B. D. PATTERSON, G. M. MIKKELSON, A. CUTLER, AND W. ATMAR. 1998. A comparative analysis of nested subset patterns of species composition. Oecologia 113: 1–20.

YOUNG, K. R., AND C. REYNEL. 1997. Huancabamba Region, Perú and Ecuador. *In* S. D. Davis, V. H. Heywood, O. Herrera-MacBryde, J. Villalobos, and A. C. Hamilton (Eds.). Centers of Plant Diversity, a guide and strategy for their conservation, Vol. 3. The Americas, pp. 465–469. IUCN Publications Unit, Cambridge, UK.