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**THE ROLE OF LOCAL AND REGIONAL FACTORS IN THE FORAGING
ECOLOGY OF BIRDS ASSOCIATED WITH *POLYLEPIS* WOODLANDS**

**THE ROLE OF LOCAL AND REGIONAL FACTORS IN THE FORAGING
ECOLOGY OF BIRDS ASSOCIATED WITH *POLYLEPIS* WOODLANDS**

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Master of Science, University of Missouri at St. Louis, St. Louis-August 1995

A dissertation submitted to the Graduate School of the
University of Missouri at St. Louis
in partial fulfillment of the requirements for the
Doctoral degree in Arts and Sciences

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ABSTRACT

THE ROLE OF LOCAL AND REGIONAL FACTORS IN THE FORAGING ECOLOGY OF BIRDS ASSOCIATED WITH *POLYLEPIS* WOODLANDS

Understanding the extent to which patterns of functional structure and organization are repeated in space and time and the level or scale at which different factors (local and regional) operate to explain community patterns are of central importance in studies of community ecology.

In this dissertation, I studied the extent of spatial variation in foraging ecology of birds in the *Polylepis* community, a unique vegetation association of the Andes, in regard to variation in local (e.g., vegetation structure, floristic composition, food resource availability) and regional factors (e.g., biogeography). I used a pluralistic approach with detailed studies of foraging ecology of nine insectivorous bird species (and the assemblage they conform) across twelve disjunct *Polylepis* woodlands embedded in three biogeographic regions of the Peruvian Andes. I focused the study on foraging ecology (i.e., maneuvers and microhabitat use) because the ways in which individuals forage influenced their performance. Natural selection should favor those strategies that maximize fitness, or some proxy of fitness, e.g., rate of resource acquisition, production of offspring.

I examined the extent of spatial variation in foraging ecology at species and assemblage levels. At species level, I assessed intraspecific variation using two foraging niche components: breadth and plasticity, both of which provide complementary information at different spatial scales and levels of organization (e.g., species, populations). Niche breadth measures if the species is a specialist (i.e., uses a relatively limited fraction of the range of available resources) or generalist (i.e., uses a relatively large fraction of available resources) relative to other community members or species in a clade. Niche plasticity evaluates how restricted or plastic are intraspecific regularities in the niche. Thus, a species is restricted if its niche is consistent across populations, and plastic when niche regularities across populations break down. Results indicate that foraging niches of bird species varied in a continuum from specialist-restricted (i.e., consistently narrow foraging niche) to generalist-plastic (i.e., highly variable and broad niche). With the exception of one specialist-restricted

species (*Oreomanes fraseri*), foraging ecology of bird species seemed to be influenced mostly by fluctuations in food resources, floristic composition, and vegetation structure. In particular, variation in food resources was a predictor of foraging ecology in seven of the nine bird species studied. Lack of variation in foraging of specialist-restricted species, despite fluctuations in local factors, may be a consequence of past events in the evolutionary history of the species that set a limit to the range of possible responses within a population, constraining the foraging niche.

At the insectivorous assemblage level, I assessed variation in structure using the conventional guild approach (e.g., guild classification, number of guilds) with the underlying assumption that species with similar ecological attributes act or respond to environmental variation in similar ways. I focused on two factors that may influence assemblage structure: food resources (i.e., arthropod abundance in microhabitats where birds forage) and the potential effect of biological interactions (i.e., competition). The relative importance of food resources was assessed by relating site similarities in food resource abundance and site similarities in richness and abundance of birds within guilds. The potential role of competition was assessed using null models to determine if patterns of niche overlap among species in the assemblages were consistent with competition theory. Results indicate that niche overlap patterns in the assemblage may respond to competitive interactions (i.e., assemblage niche overlap was significantly higher than expected by chance). However, food resources seemed to be of relative less importance in structuring bird assemblages in the *Polylepis* community. Guild identities were largely consistent among *Polylepis* woodlands, with bark foragers, foliage foragers, and aerial foragers present at most sites. However, the number and identity of species associated with each guild was not necessarily consistent due to regional differences in species richness and intrapopulation variation in foraging ecology. Studies that describe the extent of spatial variation in the structure of communities and the factors in which the community is embedded are insightful, yet scarce. The present study acknowledges the complexity of communities as a dynamic collection of species integrated to varying degrees by ecological and historical factors.

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INSECTIVOROUS BIRD SPECIES ASSOCIATED WITH *POLYLEPIS*
WOODLANDS IN THE ANDES OF PERU



CHAPTER ONE

LOCAL AND REGIONAL PATTERNS OF FLORISTIC COMPOSITION AND VEGETATION STRUCTURE OF *POLYLEPIS* WOODLANDS IN THE PERUVIAN ANDES

The relative contribution of local, regional and historical processes in structuring biological communities continues to be a debated issue in community ecology (Latham and Ricklefs 1993, Ricklefs and Schluter 1993, Francis and Currie 1998, Ricklefs and Latham 1999, Kelt 1999). Local contemporary processes have often been invoked to be of prime importance in structuring extant communities and, therefore, community attributes are expected to be strongly correlated with particular local physical and biotic features (Connell 1978, Huston 1979, Keddy 1989, Palmer 1991, Zobel 1992, Aarssen 1992, Tilman and Pacala 1993). In recent years, conceptual models of community structure have broadened, and patterns and processes on regional (i.e., biogeography) and historical (i.e., history of taxa) levels have also been considered to structure ecological communities (Ricklefs 1987, Cornell and Lawton 1992, Ricklefs and Schluter 1993, Schluter and Ricklefs 1993, Losos 1994, Caley and Schluter 1997, Karlson and Cornell 1998, Losos et al. 1998).

Studies on several taxa support the hypothesis that contemporary communities are the result of the complex role of the local and regional environment and the evolutionary and historical relationships of the taxa involved (e.g., Darwin's finches, Grant 1986; Caribbean *Anolis* lizards, Losos 1994, Losos et al. 1998; stream fishes, Angermeier and Winston 1998; desert rodents, Kelt 1999; plants in calcareous grasslands, Pärtel and Zobel 1999). Consequently, understanding present structure and organization of communities

require multiple analytical approaches that incorporate the local, regional, and historical factors, as well as chance events in which the community is embedded (Vuilleumier and Simberloff 1980, Ricklefs 1987, Ricklefs and Schluter 1993, Angermeier and Winston 1998). Yet, generalizations about the relative importance of particular processes in explaining community structure and organization depend to a great extent on the ability to delimit the community itself, and on an adequate knowledge of the patterns of variation of community-level attributes in space and time.

The high Andes of South America provide an ideal setting to examine the patterns of spatial variation in fundamental attributes of plant community structure such as floristic composition and vegetation structure. The diverse topography of Andean mountains results in a complex mosaic of areas that vary in microclimate, soils, aspect, exposure, and wind conditions (Walter and Medina 1969, Smith A. 1972, 1977, Smith B. 1988, Sarmiento 1986, Smith and Young 1987, Young 1992, Fjeldså and Kessler 1996, Young and León 1999), as well as frequency and intensity of natural (i.e., landslides, Gentry 1982, 1992) and anthropogenic disturbances (Ellenberg 1958a, 1958b, Laegaard 1992, Hensen 1993, Kessler 1995, Fjeldså and Kessler 1996). This complex set of local conditions creates opportunities for specialization and adaptation, and has likely led to the heterogeneous distribution of plants across the Andes (Young 1992, Young and León 1999). However, despite considerable local variation may occur in Andean systems, patterns of species distribution across regions may be more regular as a result of shared environmental history. For instance, the Andes are composed of several independent structural units separated by low valleys that represent important barriers for dispersal of high elevation elements (Simpson 1975). The movements of plants into high mountain habitats and their subsequent

speciation likely proceeded differently in each section of the Andes. Therefore, the phytogeographical history of the Andean flora includes shifting climatic zones, vicariant events, dispersal of montane species, and spread of taxa from other continental floras (Chardon 1938, Vuilleumier 1971, Simpson 1975, 1983, Ruthsatz 1977, Cleef 1981, Simpson and Todzia 1990, Kessler 1995, Taylor 1995).

Throughout the high Andes of Peru (ca. 3500-4800 m), forests dominated by the arborescent genus *Pohlylepis* R. & P. (Rosaceae) formed a distinctive and clearly defined community of exceptional interest in ecology and biogeography. In this community, woodlands dominated by one and sometimes two or three sympatric *Pohlylepis* species (characterized by gnarled shape with thick and rough, densely laminated bark) occur as small islands in gorges, on slopes, and along cliff edges. The microclimate, productivity, and species composition of the woodlands contrast sharply with surrounding grassland habitats (Weberbauer 1945, Troll 1959, Koepcke H. 1961, Simpson 1979, Vuilleumier 1984, Smith D. 1988, Kessler 1995, Fjelds  and Kessler 1996). Contemporary patterns of distribution of *Pohlylepis* woodlands have been attributed to microclimatic and physiological requirements of the plants (Weberbauer 1945, Troll 1959, 1968, Koepcke H. 1961, Walter and Medina 1969, Simpson 1979, Vuilleumier 1984, Rauh 1988). Alternatively, it has been suggested that these woodlands are relicts of a habitat that was more widespread during the late Pleistocene (*i.e.*, 10,000-20,000 years ago) and has become fragmented due to anthropogenic disturbances (Ellenberg 1958a, 1958b, Beck and Garcia 1991, Fjelds  1992a, Hensen 1993, Kessler 1995).

The scattered distribution of *Pohlylepis* woodlands throughout the Andes provides a set of discrete and relatively simple systems in terms of plant species composition, when

compared to more species-rich forests at lower elevation, thus facilitating studies on floristic composition and vegetation structure.

To date, few studies have looked at patterns of spatial variation in floristic composition and vegetation structure within a local and regional context (Gentry 1982, 1992, 1995, Hensen 1993, Dillon et al. 1995, Sklenar and Jorgensen 1999). Therefore, little is known about the relative importance that particular local and regional processes play in structuring Andean communities. Describing patterns of floristic composition and vegetation structure in contemporary *Polylophus* woodlands is of considerable importance to determine the potential mechanisms that likely generate and maintain the structure of the plant assemblage in this community. Local contemporary patterns of floristic composition and vegetation structure in *Polylophus* woodlands might stem from local conditions that favor the presence of some species in some sites more than in others. Consistent patterns in the relationship of local floristic composition or vegetation structure to site conditions would support the hypothesis that local processes are the major determinants of plant assemblage organization. Conversely, local patterns of floristic composition and vegetation structure may also stem from regional factors such as large-scale environmental conditions or physical/biotic barriers to dispersal, in addition to the history of the taxa that make up the assemblage. Similar patterns of floristic composition and vegetation structure in *Polylophus* woodlands within, but not among regions would provide support for a major role for regional and/or historical processes in determining plant assemblage organization.

The present study is aimed toward documenting the degree of spatial variation in floristic composition and vegetation structure of plant assemblages across a series of *Polylophus* woodlands located in three regions of the Peruvian Andes. The main objectives are: (a) to

describe how *Polylepis* woodlands vary in floristic composition and vegetation structure across sites and regions, (b) to determine the scale (local and/or regional) that best explains patterns of floristic composition and vegetation structure, and (c) to develop hypotheses regarding the potential causal mechanisms (processes) that influence patterns of floristic composition and vegetation structure in *Polylepis* woodlands and the scale at which they operate.

METHODS

Regional settings

The Andes are differentiated longitudinally into a series of parallel mountain systems divided along their length into distinct tectonic segments recognizable by surface and structural features, volcanism, geophysical evidence, and boundaries (Jenks 1956, Petersen 1958, Ham and Herrera 1963, James 1971, Simpson 1975, Smith D. 1988). Three different regions of the Peruvian Andes were selected for the present study: the Cordilleras Blanca, Occidental, and Vilcanota. The Marañon River separates the western Cordillera Occidental, and the eastern Cordillera Oriental (James 1971, Smith 1988) between the Huancabamba and Abancay deflections (Fig. 1). Each of these mountain systems is composed of a series of segments. The northern portion of C. Occidental (Ancash Department) is C. Blanca. Towards the south, (Lima Department) there is a separate segment, hereafter called C. Occidental (Fig. 1). C. Oriental is also composed of separate segments, including Cordillera Vilcanota, one of the three study regions (Fig. 1). Despite geological differences, all these mountain systems reached their present altitude in the Pleistocene or late Tertiary.

The regions selected for this study are recognized to differ biogeographically (Koepcke H. 1961, Koepcke M. 1961, Simpson 1975, Berry 1982, Lamas 1982, Smith D. 1988, Fjeldså 1992a, 1992b, 1993). In addition, C. Blanca and C. Vilcanota have been hypothesized to be glacial Pleistocene refuges for a number of taxa (Fjeldså and Kessler 1996) and areas of ecoclimatic stability that have promoted speciation processes (Fjeldså et al. 1999).

The climate in tropical mountains is characterized by small annual variation in mean temperature, large variation of daily temperature, and a seasonal pattern of cloudiness and precipitation (Johnson 1976, Sarmiento 1986). The monthly and annual precipitation and humidity are quite variable from site to site due to topography (Kessler 1995) but in general, a dry season characterized by low precipitation and humidity occurs from late April to early November and a wet season from late November to early April, when moisture is carried from the Amazon basin by tropical easterlies and clouds form locally by heating of slopes (Johnson 1976, Smith D. 1988). Climatic data from high mountain areas are scarce and fragmentary information on temperature, precipitation, and humidity is available only from stations located in valleys (Smith, D. 1988, Arce 1992, Galiano 1995) (Fig. 1).

Local settings

Within each region, I selected four *Pohlylepis* woodlands > 50 ha in size and above 3500 m elevation. At these elevations, distinct woodlands dominated by *Pohlylepis* species and separated by Puna grasslands are a prominent feature of the landscape (Lamas 1982, Kessler 1995). Sites within the same region were selected based on similarities in moisture conditions and tree architecture of dominant *Pohlylepis* species (Table 1). The 12 woodland

sites selected for the present study were: 1) C. Blanca: Aquilpo and Ishinca (dominated by *P. weberbauerii*), Morococha and Llanganuco (*P. sericea*); 2) C. Occidental: Maticuna and Japani (*P. incana*), Yauí and Quichas (*P. weberbauerii*); and, 3) C. Vilcanota: Yanacocha, Sacsamonte, Pumahuanca, Quenuamonte (*P. racemosa*) (Fig. 1).

General study design

I studied floristic composition and vegetation structure using a hierarchical sampling design with four independent woodlands within each of three regions (Cordillera Blanca, C. Occidental, and C. Vilcanota) (Total woodlands = 12). In each woodland, two sets of four transects (100 m length and placed 50 m apart from each other) were established in the forest interior (hereafter referred as plots), separated by at least 500 m (Total plots = 24). Each plot was located in a homogeneous place regarding aspect and degree of slope. Data on floristic composition and vegetation structure were taken in eight randomly placed 20 x 5 m belts embedded within the four main transects on each plot (covering a total of 0.08 ha). Data were combined across the eight 20 x 5 m belts; the experimental unit was each plot.

Floristic composition and vegetation structure

Data on floristic composition and vegetation structure were taken across *Pohlylepis* woodlands from May to December 1997, months that correspond to the dry season and beginning of the rainy season. Since *Pohlylepis* species and most vegetation are evergreen, changes in season are not expected to have a great impact in the present study.

Floristic composition.- To compare floristic composition across study plots and woodlands I identified all trees (>10 cm dbh) and shrubs (<10 cm dbh and > 50 cm height)

found in belt transects. The presence (“1”) or absence (“0”) of each plant species was then included in a plot by plant species matrix for analyses. I built a “floristic composition distance matrix” to obtain a measure of resemblance between plot pairs using Sorensen’s similarity coefficient. I used species accumulation curves to examine whether the number of plant species reached an asymptote. Voucher specimens for all woody plant species were collected and deposited at the Vargas Herbarium at Universidad Nacional de San Antonio Abad in Cusco, and the Weberbauer Herbarium at Universidad Nacional Mayor de San Marcos in Lima.

Vegetation structure.- Aspects of vegetation structure were derived based on measurements of all woody plants (> 50 cm height). The following structural variables were calculated to obtain a single measure for each plot per site:

a. Tree size class and mean tree height (HEIGHT).- I measured dbh and height for each tree in belt transects. I assigned trees to one of three size categories: > 10-20 cm dbh (DBH1), > 20-30 cm dbh (DBH2), and > 30 cm dbh (DBH3). Height was measured for each tree encountered using a telemetric graduated pole (12 m, Hastings Telescoping Measuring Rod); mean tree height was then calculated at the plot level. For analyses, I combined measures of all trees regardless of species identity.

b. Total basal area (TBA).- I used basal area as a measure of tree species coverage. TBA was calculated by converting measures of diameter at breast height (dbh) of all trees to circular area. Tree basal area was then summed across transects to obtain TBA per plot (800 m²).

c. Tree density (TD) and shrub density (SD).- I counted the number of trees (> 10 cm dbh) within each of the eight 20 x 5 m belts, summed values across all belts within a plot

and divided the total by the area of the plot (800 m²) to get density estimates. I estimated density of shrubs (< 10cm dbh and > 50 cm height) in a similar manner.

d. Foliage height density (FHDEN) and foliage height diversity (FHD).- Every 20 m along each of the four 100 m transects within a plot (total n = 24 points per plot), I took measurements of foliage height density along "vertical" transects with a telemetric graduated pole. The number of times vegetation "intersected" the pole in a radius of 25 cm was recorded at the following intervals: 0-2 m (FHDEN1), > 2-6 m (FHDEN2), and > 6-10 m (FHDEN3). Vegetation contacts were summed within each interval across points and then divided by total contacts across all heights to obtain a proportion of foliage density occurring within different heights. The proportion of the vegetation in each interval was used to calculate foliage height diversity values using the Shannon-Wiener Index (MacArthur and Horn 1969, James and Shugart 1970).

I built a "vegetation structure distance matrix" to obtain a measure of resemblance between plot pairs using Sorensen's dissimilarity coefficient.

Local factors

Many local factors have been suggested to account for contemporary patterns of distribution of *Polylepis* woodlands, including features related to topography, edaphic conditions and microclimate (Simpson 1979, Smith D. 1988, Kessler 1995). Microclimatic data for *Polylepis* woodlands, however, and for most Andean forests, is lacking. For the present study, local conditions were based on a qualitative assessment of each plot. I obtained data on two topographic features: degree and aspect of slope; and one edaphic feature: soil texture (Table 1).

Topography.- The aspect and degree of slope influence the amount of solar radiation received, hence the temperature and moisture regimes (Smith D. 1988). I measured aspect and degree of slope with a compass and categorized aspect (1=SW, 2=W, 3=N, 4=S, 5=E, 6=NE) and degree of slope (1=50-60°, 2=30-45°, and 3=10-20°) at each plot.

Edaphic conditions.- High Andean soils have variable texture, and the distribution of plant species may respond to soils with different levels of stone coverage, since previous studies have shown that stones provide protection mainly due to an increase in soil temperature (Smith D. 1988). Soil texture was categorized by the percent cover of stones on the ground; categories included: 1=>50% coverage, 2=>10-50%, and 3=<10%.

Data obtained from local factors were used to construct a “local distance matrix” using Sorensen’s dissimilarity values between plot pairs.

Regional factors

The study relies on the integration of floristic composition and vegetation structure patterns nested within three distinct biogeographic regions. I built a “regional distance matrix” by examining each plot pair and scoring “0” if plots belong to same region and “1” if they differed.

Geographic distance

I included a measure of geographical distance to understand overall trends of floristic composition and vegetation structure. I used a map of the Peruvian Andes and measured the linear distance between the 276 possible pair plots, with the aid of Geographic Information Systems (ESRI 1992-1997) to build a “geographic distance matrix”.

Data analysis

I analyzed data on floristic composition and vegetation structure of *Polylepis* woodlands using univariate and multivariate statistics. I used a combination of hierarchical Analysis of Variance (*ANOVA*), Bray Curtis ordination techniques, and *Mantel* tests to assess the relative importance of the local and regional factors in explaining patterns of floristic composition and vegetation structure.

Rarefaction curves.- I used rarefaction analyses (Hurlbert 1971, Simberloff 1972, Gotelli and Graves 1996) to build species accumulation curves using the EcoSim Program, Version 5.53 (Gotelli and Entsminger 2000). The program draws a designated random sample of individuals from a given species abundance distribution to estimate species richness in regard to sampling effects. Simulations were repeated 1000 times to provide mean, variance and 95% confidence intervals of species richness at each forest plot based on different abundance levels to facilitate comparisons among woodland sites and regions.

Analysis of variance models.- To examine if patterns of vegetation structure vary in woodlands nested within region or across regions, I used a General Linear Model (GLM) (*SPSS* 1999) to do hierarchical Multivariate Analysis of Variance (*MANOVA*) that included 11 vegetation structure variables (TBA, TD, SD, FHDEN1, FHDEN2, FHDEN3, FHD, HEIGHT, DBH1, DBH2, and DBH3). I used the same analysis of variance model to examine floristic composition, including total plant species number and total number of individuals as variables. Normality of each variable was tested using Wilk-Shapiro tests and variables were logarithmically transformed when necessary. Plots within woodlands were used as replicates in the design and the null hypothesis was that vegetation structure variables did not differ across woodlands or regions. More specifically, a significant among

group ($F_{2,9}$) component will indicate the relative importance of regional factors (*i.e.*, large-scale environmental conditions, physical/biotic barriers to dispersal, and history of the taxa) in explaining floristic composition and vegetation structure patterns. If "among forests within regions" component ($F_{9,12}$) is found to be significant, then this will indicate the relative importance of local factors (*i.e.*, aspect and exposure of slope, soil texture) in shaping floristic composition and vegetation structure. If both terms were found to be significant then both local and regional processes could be implicated as important predictors of vegetation structure patterns in *Polylepis* woodlands. Results of hierarchical *MANOVA* were followed by Tukey tests to identify which woodlands and regions were significantly different from each other.

Bray Curtis ordination.- I analyzed patterns of similarity in floristic composition among forest plots independently from patterns of similarity in vegetation structure variables using Bray Curtis ordination (PC-ORD Version 4, McCune and Mefford 1999). I used Sorensen's percent dissimilarity as a measure of distance between plots. This index is commonly used with ecological data because it retains sensitivity in heterogeneous data sets and gives less weight to outliers (McCune and Mefford 1999). I used the variance regression method for end point selection and Euclidean distance for axis projection geometry (Beals 1984, Greig-Smith 1983, McCune and Mefford 1999). The 11 vegetation structure variables (columns) across 24 study plots (rows) were relativized by column totals to give equal importance to all variables. The variables for the floristic composition matrix were the presence or absence of each plant species (columns) across the 24 study plots (rows).

Mantel tests.- I used *Mantel* tests, a regression approach that compares the relationship between distance matrices (Mantel 1967, Burgman 1987, Sokal and Rohlf 1995),

to estimate the relative effect of local and regional processes among woodlands or regions in terms of floristic composition and vegetation structure. Analyses were run using the program *Permute* version 3.4, release alpha 5 (Casgrain 1998), a special version of *Mantel* test which allows for several predictor variables to be tested over one response variable and generates partial regression coefficients and the associated permutation probability for each predictor variable.

Floristic composition and vegetation structure were the response variables and were represented by distance matrices generated using Sorensen's percent dissimilarities. Two separate models were tested, the floristic composition model included three predictor variables: 1) region (built by examining each plot pair and scoring "0" if plots belong to same region, and "1" if they differed), 2) geographic distance (built using the actual distance (in km) between the 276 plot pair combinations); and 3) local variables (a dissimilarity matrix based on measurements at each plot). The vegetation structure model included: 1) region, 2) geographic distance, 3) floristic composition (since plant composition may influence physiognomy), and 4) local conditions, as predictor variables. I selected the variable(s) that most contributed to explaining variation in structure or composition dissimilarity matrices using stepwise regression followed by a backward elimination procedure; 999 permutations of the original matrix were performed to determine the significance probability of the observed relationship between predictor and response variables data matrices.

RESULTS

Floristic composition patterns

The forest interior of *Polylepis* woodlands contained a total of 56 plant species distributed among 34 genera and 21 families. Asteraceae was by far the most speciose family (22 species), and within Asteraceae, the most speciose genera were *Baccharis* (6 species) and *Gymoxys* (6 species) (Appendix 1.1). At least 28 genera were represented by only one species. From the total list of plant species, 30% (17 species) are restricted to high elevations above 3000 m and 23% (13 species) are considered endemic to the Peruvian Andes (Brako and Zarucchi 1993) (Appendix 1.1).

Plant species sampling in most plots approached an asymptote as revealed by accumulation curves (Fig. 1.2). Accumulation curves also illustrate the great variation in plant species richness across sites and regions. When number of individuals is controlled for, plant species richness differs significantly across *Polylepis* woodlands and regions (Table 1.2). Basically, more species were found in Llanganuco (average 12 plant species/100 individuals), and one plot in Morocochoa (average 8 species /100 individuals) (Cordillera Blanca), and Yanacocha (average 12 species/100 individuals) (C. Vilcanota) than in other woodland sites (Fig. 1.2, Table 1.2). In addition, hierarchical *MANOVA* of total number of species and individuals at each plot revealed significant differences across *Polylepis* woodlands (Table 1.3), as well as among regions, with C. Occidental contributing to the difference in species and individuals number (Table 1.3).

Sorensen's percent dissimilarity values between woodlands (plots within woodlands combined) ranged from 0 - 0.52 (0 indicates no similarity, 1 equal or high similarity) (Fig. 1.

3). Results emphasized that forests within the same region tended to be similar in floristic composition yet regions differed floristically. Similarity values were low even within same region not only due to differences in plant species composition but also, in most cases, to differences in species richness in woodlands within the same region. For example, in C. Occidental, Quichas and Yauí were sites with low species richness that did not share any species (including *Polylepis*) with Japani, resulting in low similarity values between these sites (Fig. 1.3).

Bray Curtis ordination of a presence/absence matrix of 53 plant species across 24 plots revealed similarities in floristic composition within regions (Fig. 1.4). The first three ordination axes explained 59% of the variance. Axis 1 (29% variation) separated plots in C. Vilcanota from plots in C. Blanca and C. Occidental (Fig. 1.4). Axis 2 (15%) separated Ishinca plots from Maticuna (Fig. 1.4), and axis 3 (15%) separated Morococha and Llanganuco plots from Yauí and Quichas plots. Different species of *Baccharis*, *Berberis*, *Gynoxys*, and *Polylepis* had high factor loadings in the two first axes of the ordination, and therefore contributed to regional separation.

Region and geographic distance explained a large proportion of the variance in floristic composition as revealed by Mantel test (Table 1.4). A significant positive association between floristic composition and geographic distance indicates that *Polylepis* woodland plots closer together share more species than plots further apart, and that plots within regions are more similar than plots among regions (Table 1.4). Local factors accounted for only 8% of the variance in floristic composition (Table 1.4).

Vegetation structure patterns

In general, woodlands dominated by *Polylepis racemosa*, *P. weberbauerii* and *P. sericea* were more similar structurally than woodlands of *P. incana*. However, in most cases, plots from different woodlands showed greater similarity than did plots within the same woodland (e.g., Morococho, Quenuamonte, and Pumahuanca, Fig. 1.5), suggesting some degree of local heterogeneity.

Results of the ordination revealed that axis 1 (51%) largely separated *Polylepis* plots located in the three regions of study from a set of five plots located in the C. Occidental; the latter were characterized by low total basal area and greater foliage density below 6 m (Table 1.5, Fig. 1.5). Axis 2 (13%) separated one of the Maticuna plots (T2) from all remaining ones (Table 1.5, Fig. 1.5). This plot was characterized by greater foliage density below 2 m (Fig. 1.5). In general, plots in *Polylepis* woodlands within C. Vilcanota and C. Blanca tended to have greater basal area, larger trees, and more foliage in the canopy than Japani and Quichas in C. Occidental.

Vegetation structure in *Polylepis* woodlands differed significantly both across sites nested within regions ($F_{9,12} = 5.83$, $P < 0.01$) and across regions ($F_{2,12} = 1.86$, $P = 0.05$). All structural variables differed significantly across sites except tree density (TD) and number of small trees ($> 10 - 20$ cm dbh) (Table 1.6). I found significant differences across regions in all variables except number of small and large trees, foliage density below 2 m, and mean tree height (Table 1.6).

Patterns of vegetation structure were explained by local variables (exposure and angle of slope, and soil texture) measured at each plot, as revealed by Mantel test. Floristic composition and geographic distance also contributed to the variance in patterns of

vegetation structure in *Pohlylepis* woodlands (Table 1.4). As geographic distance among plots increases, plots are more similar in vegetation structure. This result agrees with the Bray Curtis ordination in which plots of *Pohlylepis* woodlands located within C. Blanca and C. Vilcanota, the two more distant regions in the present study, tend to group together.

DISCUSSION

The role of local and regional factors as significant predictors of floristic composition and vegetation structure in *Pohlylepis* woodlands is summarized in Figure 6. Regional factors, including history, had important influences on floristic composition but only contributed indirectly (through their effect on floristic composition) to explain vegetation structure. Instead, floristic composition and local conditions played a more important role in determining vegetation structure. In sum, the floristic composition component of communities, influenced by large-scale environmental and historical processes, further interacts with local environmental conditions to influence the physiognomy of the vegetation (cf., Pärtel and Zobel 1999).

Floristic composition

Patterns of floristic composition similarities in *Pohlylepis* woodlands were strongly influenced by regional factors and to a lesser extent by local factors. Floristic composition in *Pohlylepis* woodlands might be linked to present environmental conditions that are shared within a region, such as precipitation, temperature, and humidity, as has been reported in many studies in other systems and regions of the world (e.g., Gleason and Cronquist 1964, Good 1974, Grace 1987, Sykes et al. 1996, Bullock et al. 2000). Indeed, the regions selected

for the present study vary in humidity, and it has been proposed that species richness in *Polylepis* woodlands is higher in more humid areas (e.g., C. Blanca and C. Vilcanota) than less humid ones (e.g., C. Occidental) (Fjeldså 1992a, 1992b, 1993, Fjeldså and Kessler 1996). However, even though current environmental conditions may explain patterns of plant species richness, they do not necessarily account for patterns of floristic composition turnover across regions (Fig. 1.3).

Present distribution of plants inhabiting *Polylepis* woodlands and similarities within but not across regions suggests a greater role for environmental history as a determinant of present day floristic composition. One of the major determinants of floristic composition changes in recent earth history was the cyclic change in climate and topography during the Pleistocene (see explanation in terms of global cooling and orbital forcing by Berger et al. 1984, Shackleton et al. 1990, and Hooghiemstra and Ran 1994). Many Cordilleras in Peru were covered by ice repeatedly over the last 2-3 million years, restricting plant species to lower elevations on the Andean slopes, and to certain mountain basins that remained ice-free (Simpson 1975, Simpson and Todzia 1990, Fjeldså and Kessler 1996). The iced-covered mountain caps may have isolated some refuges with *Polylepis* woodlands and associated vegetation from the continuous band of humid shrubbery that is thought to have remained along the Andes. Isolation during glaciations may have promoted differentiation in certain genera (e.g., *Polylepis*, *Gymoxys*), such that distinct species evolved, remaining endemic to their area of origin (Fjeldså and Kessler 1996). These relict populations that survived periods of global climatic change likely were the source pool of species for colonization of other areas as the glaciers receded (Simpson and Todzia 1990, Fjeldså et al. 1999).

In addition, the low floristic composition similarity levels between C. Blanca and C. Vilcanota observed in the present study could also be attributed to the hypothesis that *Polylepis* woodlands were disrupted by tectonics and erosion that created isolation barriers (e.g., Apurímac Canyon, Fig. 1.1). Such vicariant events preceding Pleistocene glaciations might have served to isolate relatively non-vagile plants, resulting in pairs of sister taxa on both sides of each barrier, and thus, influencing community composition across regions. In contrast, more vagile species are likely to have been less affected because of their ability to disperse across unsuitable habitats. In such cases, one might expect to see a distance gradient in community similarities. C. Blanca and C. Occidental were the two regions that shared relatively more plant species (than did either region with C. Vilcanota). Moreover, a gradual decrease in species number from north to south suggests a relative larger role for dispersal between these two regions. Dispersal during interglacial periods and post-glacial periods could have been an important influence in explaining present floristic composition patterns (Simpson 1975, Fjeldså and Kessler 1996). The low similarity value between C. Blanca and C. Vilcanota (0.07 %) could be due to very few species with a wide distribution throughout the Peruvian Andes that were present before vicariant events, or that dispersed but were not found in the study area. Further studies are needed to address the history of taxa, a factor that may contribute with the high percent (53%, Table 1.4) of unexplained variance found in the present study. Also, tests of biogeographic relationships in which plant species for which putative phylogenetic reconstructions are available need to be compared using cladistic analyses (e.g., Brundin 1988, Humphries et al, 1988). In addition, timing of phylogenetic events (i.e., application of molecular clocks) would also be basic to

discern the relative importance of dispersal and vicariance hypotheses. To date, no parallel examples for adequate testing exist for plant taxa of the Andes.

The relative influence of local factors in determining present patterns of floristic composition similarity in *Polylepis* woodlands was small but significant ($b = 0.09^*$). This result is not surprising given that few processes could be considered uniquely regional in scale (Huston 1999). Several studies have addressed fine-scale correlations between different plant groups and local conditions (Johnston 1992, Clark D. A. et al. 1995, Clark D. B. et al. 1998, Sabatier et al. 1997, Vormisto et al. 2000). Local factors in Japanese forest could have resulted in low species richness and high turnover patterns with respect to other sites in C. Occidental (Fig. 1.4). In this study, some plant species may be locally adapted to specific soil texture, topographic positions, and slope angle.

Vegetation structure

Throughout the study area, *Polylepis* woodlands differed in vegetation structure, and patterns were influenced by floristic composition and local conditions. The influence of floristic composition on vegetation structure was expected given the fact that the combination of plant species present in a community likely contributes to its architecture and physiognomy. Yet, local conditions, such as aspect, degree of slope and soil texture affect plant growth, and other structural components of the vegetation. The overall variation in physiognomy of *Polylepis* woodlands throughout the study area is likely a consequence of variation on the morphology and growth forms of *Polylepis* trees because of their dominance in the system. Local factors measured in the present study, such as aspect and degree of slope and soil texture, have been shown to influence local abundance and

growth patterns (*i.e.*, height, branching patterns) of *Polylepis* and other plant species (Kahn 1987, Smith 1988, Clark D. A. et al. 1995, Clark D. B. et al. 1998, Fjeldså and Kessler 1996). For example, in C. Blanca *Polylepis weberbauerii* is found as dense woodlands in which trees reach 12 m height. In other localities within the same region, however, the same species are shrub-like reaching only 6 m in height. This variation has been attributed to topographic position (dense woodlands in south-facing slopes) (Smith 1988) and soil texture (*e.g.*, growth on boulders) (Smith 1988, Fjeldså and Kessler 1996). Thus, greater similarities in vegetation structure among *Polylepis* woodlands located in C. Blanca and C. Vilcanota, the two more distant regions, can be explained by similarities in local abundance and growth patterns of *Polylepis* and other plant species responding to local conditions.

Certainly, other biotic and abiotic factors not measured in this study, such as microclimatic conditions, local winds (*e.g.*, Smith 1988, Young and Leon 1999), soil nutrients (*e.g.*, Johnston 1992, Tuomisto et al. 1995), other fine-scale soil conditions (*e.g.*, Clark D. A. et al. 1995, Clark D. B. et al. 1998, Sabatier et al. 1997) may be important factors influencing vegetation structure. Indeed, the high percent of unexplained variance (88%, Table 4) may be due to these factors. Nonetheless, the results of this study point to the importance of local factors in explaining patterns of variation in vegetation structure but it does not separate causal factors from correlative ones.

In summary, the present study provides the first comparative data set on floristic composition and vegetation structure of *Polylepis* woodlands on a large spatial scale (ca. 600 km). Little overlap in floristic composition across regions of study suggest a role for regional factors, including history, while local differences in vegetation structure suggests a role for floristic composition and local conditions. By using a hierarchical approach, I was able to

better discern local and regional variation in floristic composition and vegetation structure. This is the first step to generate specific hypotheses regarding the organization of high Andean communities. The study revealed that identifying the appropriate scale that shapes patterns of vegetation structure and floristic composition in the *Pohlylepis* community requires knowledge of the regional context in which it is embedded to be able to refine hypotheses and interpretations regarding community structure and organization. As ecologists continue to sort out the roles of the many processes involved in community organization, hierarchical designs that incorporate the local and regional context in which the community is embedded will become increasingly important in revealing how and where those processes operate.

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Figure 1.1. Map of the Peruvian Andes showing study regions, *Polylepis* R. & P. woodlands, and climate stations mentioned in text. The line indicates the 3,000 m elevation contour. (A) C. Blanca: 1 = Ishinca (09°22'S, 77°28'W, 4075 m, 200 ha), 2 = Aquilpo (09°21'S, 77°30'W, 3800 m, 200 ha), 3 = Morococha (09°01'S, 77°32'W, 3836 m, 100 ha), 4 = Llanganuco (09°04'S, 77°38'W, 3850 m, 100 ha). (B) C. Occidental: 1 = Yauí (10°35'S, 76°48'W, 4184 m, 200 ha), 2 = Maticuna (10°39'S, 76°50'W, 3990 m, 200 ha), 3 = Japaní (11°41'S, 76°31'W, 4140 m, 300 ha), 4 = Quichas (10°33'S, 76°46'W, 4200 m, 100 ha). (C) C. Vilcanota: 1 = Yanacocha (13°17'S, 72°03'W, 4012 m, 200 ha), 2 = Sacsamonte (13°13'S, 72°02'W, 3926 m, 100 ha), 3 = Pumahuanca (13°12'S, 72°05'W, 4110 m, 100 ha), 4 = Quenuamonte (13°11'S, 72°13'W, 3812 m, 50 ha). Climatic stations: a = Chinancocha (9°6'S, 77°40'W, 3850m, 8°C, 642mm, and 64%), b = Lampas Alto (10°0'S, 77°20'W; 4030m, 6°C, 737mm, 67%), c = Carampoma (11°38'S, 76°26'W, 3272m, 12°C, 389mm), d = Urubamba (13°18'S, 72°7'W, 2870m, 14°C, 494mm, 66%), e = Calca (13°20'S, 71°57'W, 2859m, 15°C, 437mm).

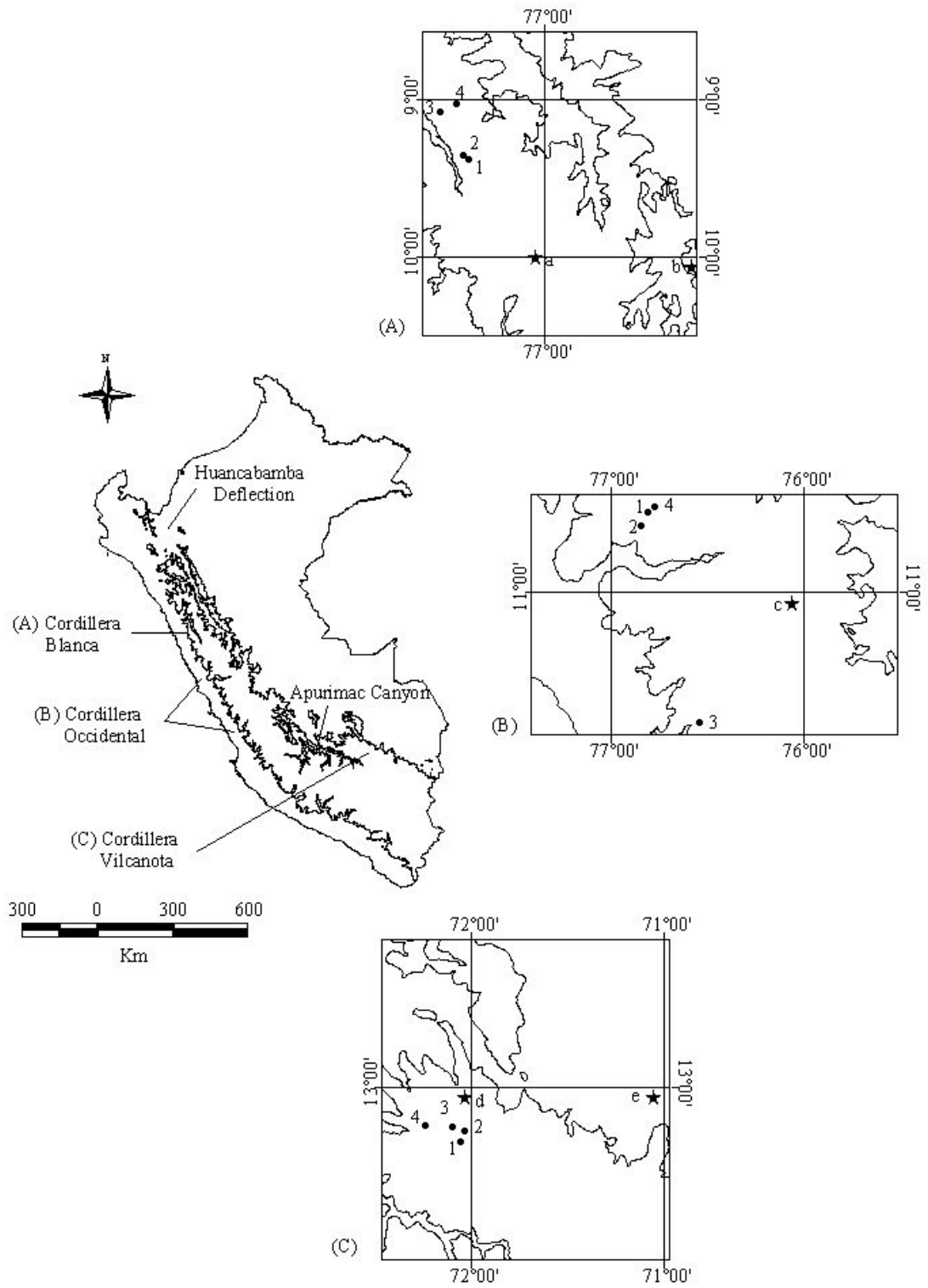


Figure 1.2. Plant species richness as a function of species abundance across *Polylepis* woodlands plots based on rarefaction analyses. (a) Cordillera Blanca, (b) C. Occidental, (c) C. Vilcanota. Labels in legend represent *Polylepis* woodlands studied (from North to South), and numbers (1 and 2) refer to plots (see text for design).

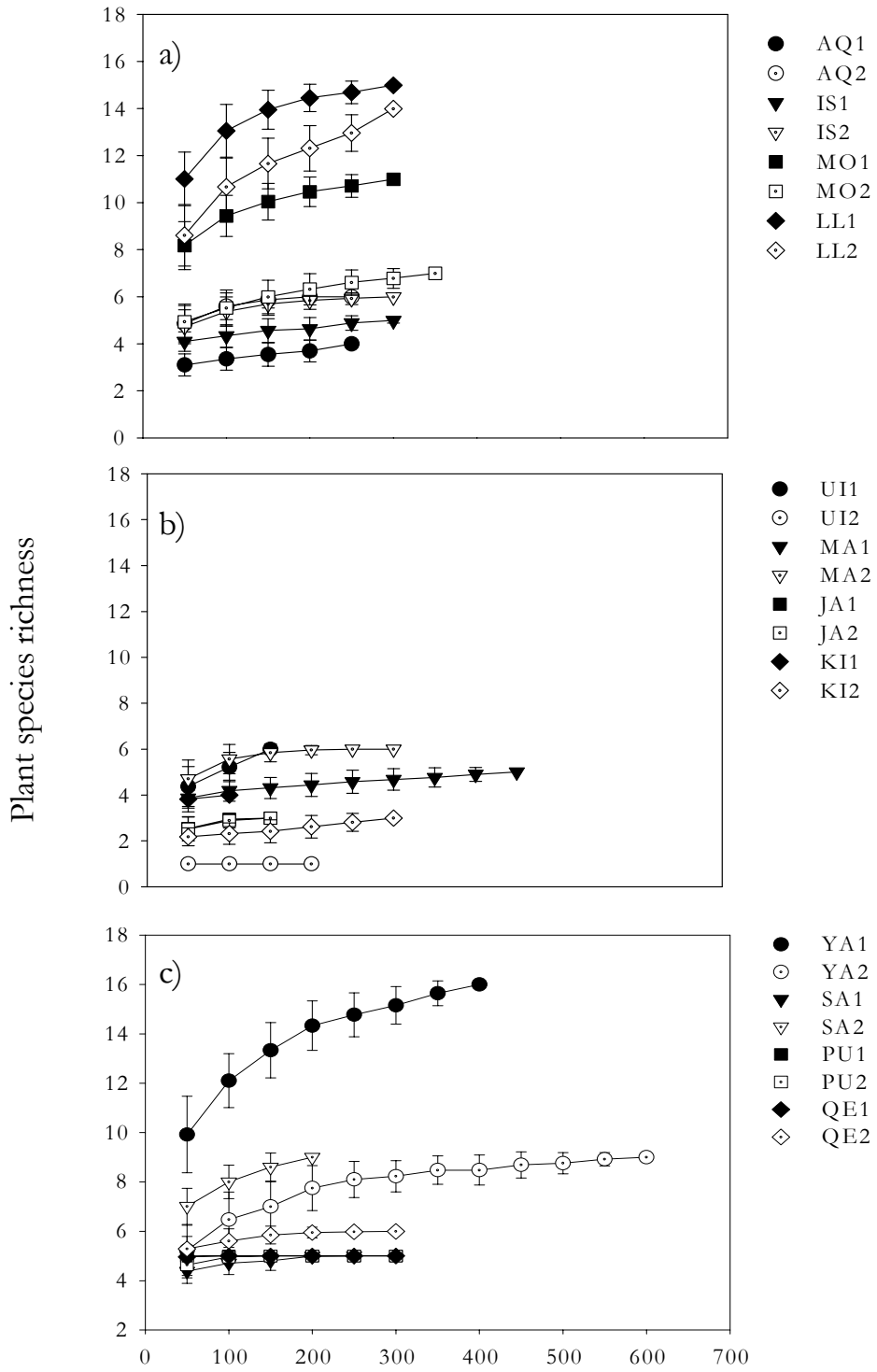


Figure 1.3. Pair-site similarities (Sorensen's coefficients) in floristic composition of *Polylepis* woodlands and regions. Higher values for Sorensen's coefficient imply greater similarity between two sites or regions.

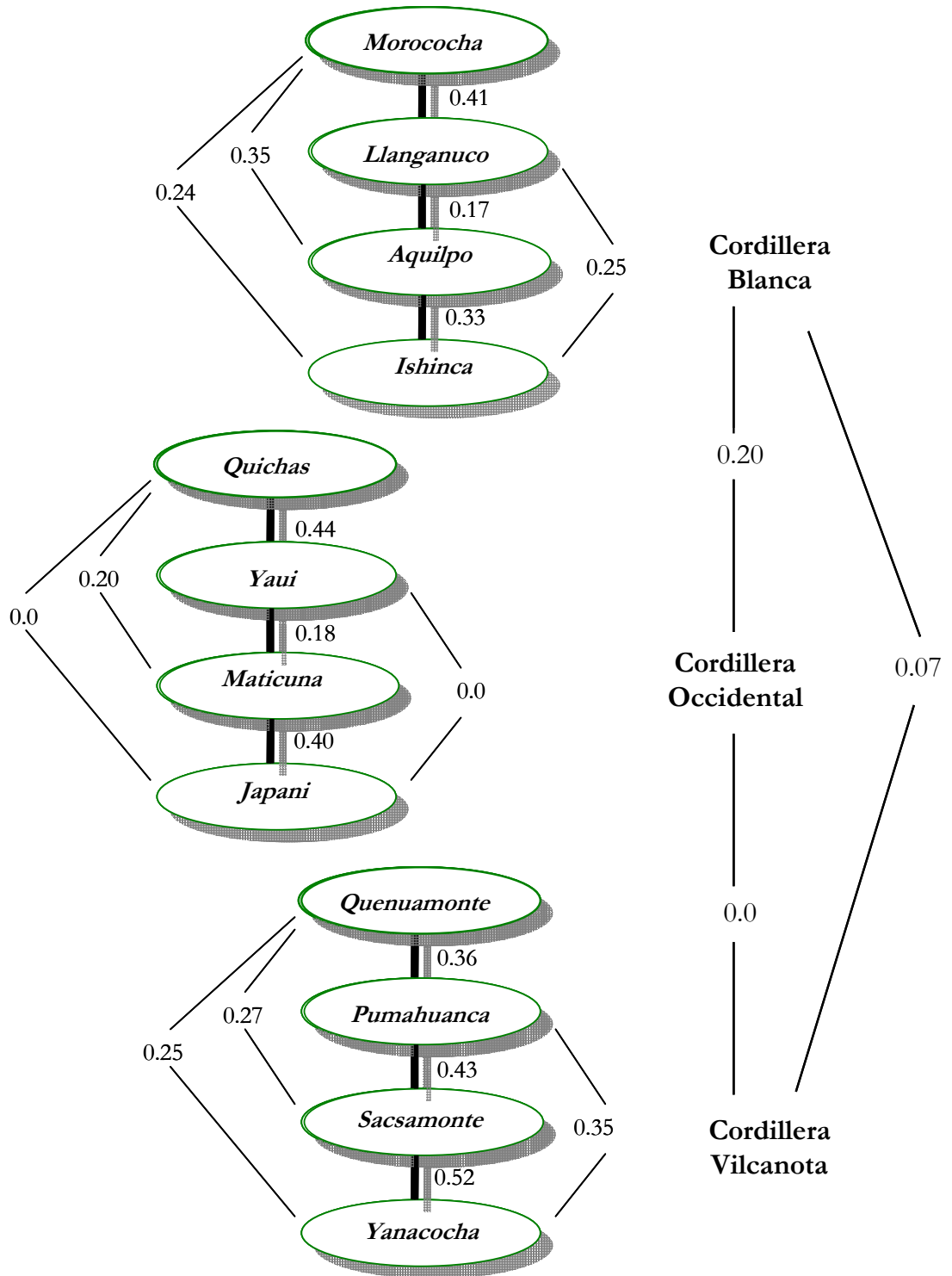


Figure 1.4. Arrangement of plots along the first and second axes obtained from Bray Curtis ordination of floristic composition (presence/absence of 53 plant species) across 24 plots. The asterisk (*) indicates endemic species to the Peruvian Andes. The letters indicate the forest: A = Aquilpo, I = Ishinca, M = Morococha, L = Llanganuco, U = Yauy, T = Maticuna, J = Japoni, K = Quichas, Y = Yanacocha, S = Sacsamonte, P = Pumahuanca, Q = Quenuamonte; and numbers (1, 2) indicate the plot.

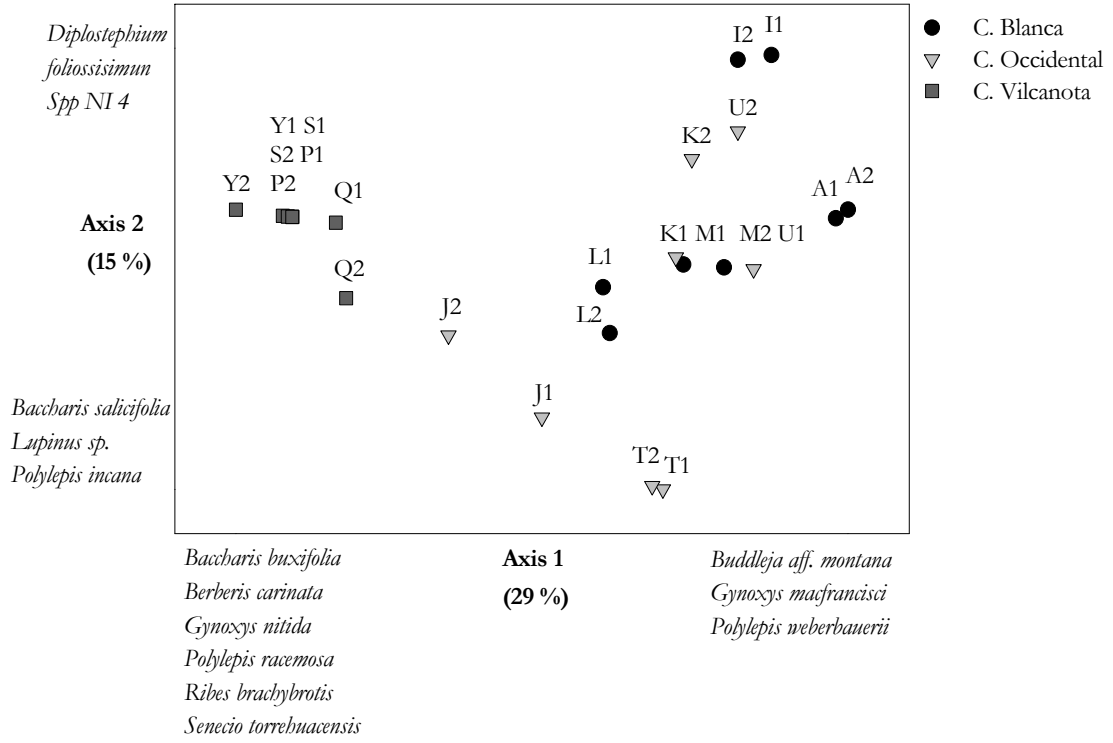


Figure 1.5. Arrangement of plots along the first and second axes obtained from Bray Curtis ordination of 12 vegetation structure variables across 24 plots. The letters indicate the forest: A = Aquilpo, I = Ishinca, M = Morococha, L = Llanganuco, U = Yauí, T = Maticuna, J = Japaní, K = Quichas, Y = Yanacocha, S = Sacsamonte, P = Pumahuanca, Q = Quenuamonte; and the numbers (1, 2) indicate the plot.

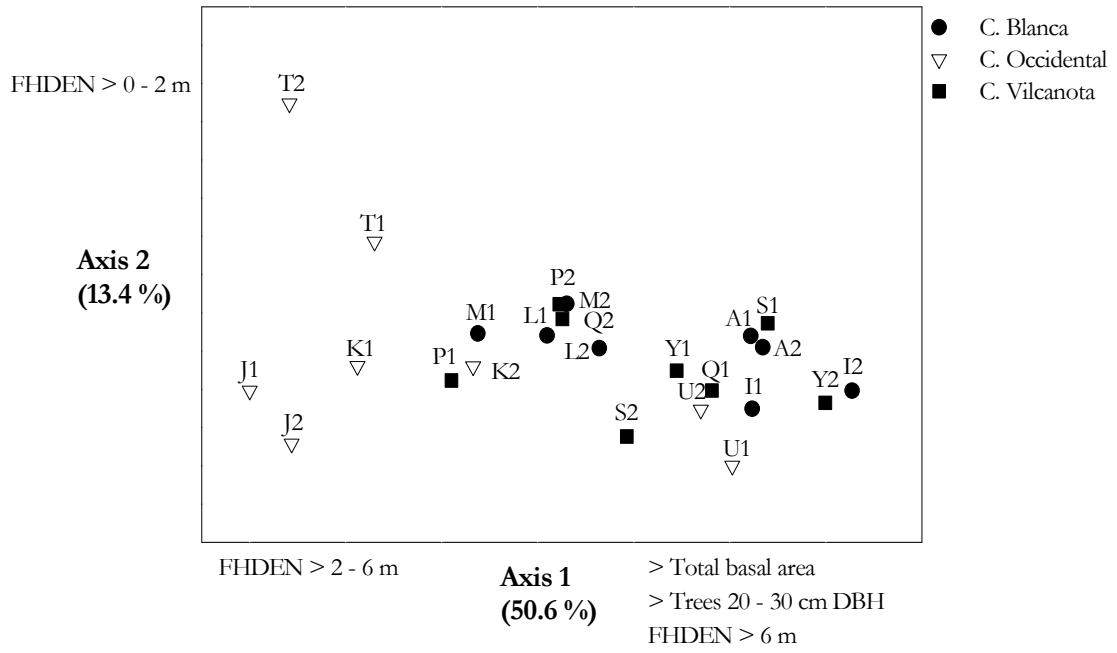


Figure 1.6. Relative contribution of local and regional factors on floristic composition and vegetation structure of *Polylepis* woodlands. Numbers are partial regression coefficients obtained from Mantel tests, and asterisks indicate significance levels: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. The contribution of each factor is emphasized by the thickness of the arrow.

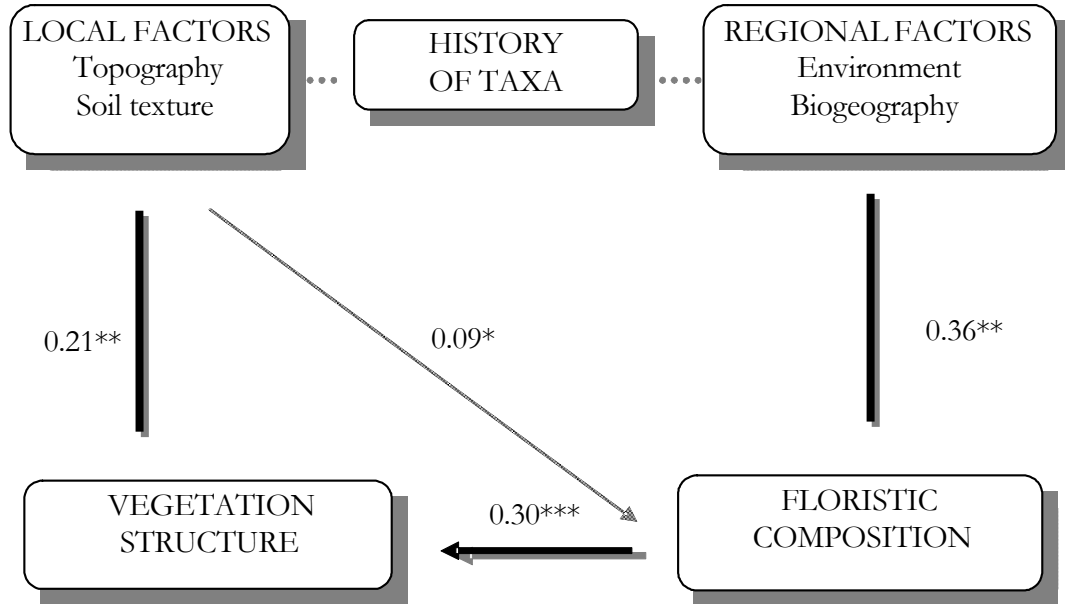


Table 1.1. *Polylepis* species present at each woodland and region and local factors measured at each plot. (1) = First notation before slash refers to plot 1 and after slash to plot 2. (2) = Categories used for stone coverage as a measure of soil texture. 1 = > 50%, 2 = > 10 – 50%, 3 = < 10% (see text).

Region	Forest	Dominant species	Exposure	Slope degree	Soil texture
C. Blanca	Aquilpo	<i>P. weberbauerii</i>	SW/SW	60/60	1/1
	Ishinca	<i>P. weberbauerii</i>	SW/SW	50/50	1/1
	Morococho	<i>P. sericea</i>	W/W	10/45	2/2
	Llanganuco	<i>P. sericea</i>	N/N	10/10	3/3
C. Occidental	Yauí	<i>P. weberbauerii</i>	S/S	60/50	2/2
	Maticuna	<i>P. incana</i>	E/W	30/35	1/1
	Japani	<i>P. incana</i>	S/S	10/10	1/1
	Quichas	<i>P. weberbauerii</i>	S/S	45/35	2/2
C. Vilcanota	Yanacocha	<i>P. racemosa</i>	E/W	60/50	1/1
	Sacsamonte	<i>P. racemosa</i>	E/W	50/50	1/1
	Pumahuanca	<i>P. racemosa</i>	NE/NE	50/20	1/1
	Quenuamonte	<i>P. racemosa</i>	E/E	45/45	1/1

Table 1.2. Mean, variance, and 95 % confidence intervals of plant species richness obtained by rarefaction after number of individuals was standardized ($n = 100$) across plots of *Polyepis* woodlands. Values were obtained after 1000 randomizations. An asterisk (*) indicates significant differences in mean species richness between plots within woodlands.

Regions	Woodlands and plots	Species Richness (X+SD)	CI (95%)	
C. Blanca	Aquilpo 1*	3.4±0.23	2.4	4.3
	Aquilpo 2*	5.6±0.32	4.5	6.7
	Ishinca 1	4.3±0.23	3.4	5.3
	Ishinca 2	5.4±0.38	4.2	6.6
	Morococha 1*	9.4±0.75	7.7	11.1
	Morococha 2*	5.5±0.59	4.0	7.0
	Llanganuco 1	13.1±1.25	10.9	15.3
	Llanganuco 2	10.7±1.49	8.3	13.1
C. Occidental	Yauí 1*	5.2±0.42	4.0	6.5
	Yauí 2*	1.0±0.00	1.0	1.0
	Maticuna 1	4.2±0.22	3.3	5.1
	Maticuna 2	5.6±0.41	4.3	6.8
	Japani 1	3.0±0.05	2.5	3.4
	Japani 2	2.9±0.10	2.3	3.5
	Quichas 1*	4.0±0.00	4.0	4.0
	Quichas 2*	2.3±0.22	1.4	3.2
C. Vilcanota	Yanacocha 1*	12.1±1.18	10.0	14.2
	Yanacocha 2*	6.5±1.26	4.3	8.7
	Sacsamonte 1*	4.7±0.21	3.8	5.6
	Sacsamonte 2*	8.0±0.46	6.7	9.3
	Pumahuanca 1	5.0±0.00	5.0	5.0
	Pumahuanca 2	5.0±0.04	4.6	5.3
	Quenuamonte 1	5.0±0.00	5.0	5.0
	Quenuamonte 2	5.6±0.24	4.6	6.6

Table 1.3. Multivariate hierarchical ANOVA results for plant species and individuals number. Means and SD are shown for both variables across 12 woodlands and 3 regions of study based on two replicate plots. Significance of F-values for local and regional effects is indicated as: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. Superscripts following means indicate differences across sites (a, b, c) or regions (A, B) according to Tukey multiple comparison among means test.

Forests and Regions	Floristic Composition Variables	
	Richness (X + SD)	Abundance (X + SD)
Aquilpo	4.5±0.70 ^{ab}	260.0±25.45 ^{ab}
Ishinca	5.0±1.41 ^{ab}	318.0±15.55 ^{ab}
Morococha	8.5±2.12 ^{ab}	338.5±30.40 ^{ab}
Llanganuco	14.5±0.70 ^c	325.0±15.55 ^{ab}
C. Blanca	8.12±4.38 ^B	310.3±36.36 ^{AB}
Yauí	3.5±3.53 ^a	187.5±19.09 ^{ab}
Maticuna	5.5±0.70 ^{ab}	379.5±102.53 ^{bc}
Japani	3.0±0.00 ^a	133.0±7.07 ^a
Quichas	3.5±0.70 ^a	253.5±108.18 ^{ab}
C. Occidental	3.8±1.72 ^A	238.3±113.58 ^A
Yanacocha	12.5±4.94 ^b	518.0±137.17 ^c
Sacsamonte	7.0±2.82 ^{ab}	214.0±31.11 ^{ab}
Pumahuanca	5.0±0.00 ^{ab}	307.5±2.12 ^{ab}
Quenuamonte	5.5±0.70 ^{ab}	332.0±5.65 ^{ab}
C. Vilcanota	7.5±3.85 ^B	342.8±129.34 ^B
<i>MANOVA</i> Local $F_{9,12}$	5.16 ^{**}	5.08 ^{**}
<i>MANOVA</i> Region $F_{2,12}$	6.17 ^{**}	9.36 ^{**}

Table 1.4. Results of Mantel tests using 999 permutations and the program Permute (Casgrain 1998). Model 1 examines the influence of local, region and geographic distance on floristic composition. Model 2 examines the influence of local, region, geographical distance, and floristic composition on vegetation structure. A significant positive value between floristic composition and geographic distance indicates that *Polylepis* woodland plots closer together share more species than plots further apart, and that plots within regions are more similar. Partial regression coefficients (b) and overall model R2 are provided. Asterisks (*) indicate significance levels. ** = $P < 0.01$, *** = $P < 0.001$.

Models	Partial regression coefficient (b)				Overall R ²
	Local variables	Region	Floristic composition	Geographical distance	
1. Floristic composition	0.09*	0.36*	---	0.37**	0.47**
2. Vegetation structure	0.21**	NS	0.30***	-0.32**	0.12**

Table 1.5. Factor loadings for vegetation structure variables along axis 1 and 2. Loadings and respective r values (in parentheses) were obtained from Bray Curtis ordination of 24 *Polylepis* plots and 11 vegetation structure variables, using Sorensen's coefficient of dissimilarity, variance-regression as endpoint selection, and Euclidean projection. DBH = Diameter at breast height (DBH1, DBH2, DBH3 = individuals number in size class 1, size class 2, and size class 3 respectively); FHD = foliage height diversity (Shannon-Wiener Index); FHDEN = foliage height density.

Vegetation Structure Variables	Axis 1	Axis 2
TBA (total basal area/m ²)	0.447 (0.876)	0.124 (-0.344)
TD (tree density/m ²)	0.396 (0.662)	0.131 (-0.336)
SD (shrub density/m ²)	0.384 (0.383)	0.155 (0.212)
DBH1 (> 10 – 20 cm dbh)	0.357 (0.177)	0.138 (-0.173)
DBH2 (> 20 - 30 cm dbh)	0.446 (0.696)	0.115 (-0.394)
DBH3 (> 30 cm dbh)	0.450 (0.447)	0.123 (-0.176)
FHD (foliage height diversity)	0.342 (-0.125)	0.140 (-0.357)
FHDEN1 (% coverage at > 0-2 m)	0.277 (-0.657)	0.191 (0.857)
FHDEN2 (% coverage at > 2-6 m)	0.274 (-0.848)	0.142 (-0.053)
FHDEN3 (% coverage at > 6-10 m)	0.442 (0.745)	0.105 (-0.588)
HEIGHT (mean tree height)	0.373 (0.483)	0.135 (-0.316)
Variation (%) extracted of the original distance matrix	50.62	13.40
Variation (%) cumulative	50.62	64.02
Sum of squares of remaining residual distances	0.018	0.013

Table 1.6. Multivariate hierarchical ANOVA results for 11 vegetation structure variables. Means and SD for all variables across 12 woodlands and 3 regions of study based on two replicate plots. Significance of F-values for local and regional effects are indicated as: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. Superscripts following means indicate differences across sites (a, b, c, d, e) or regions (A, B) according to Tukey multiple comparison among means test. TBA = total basal area (800 m²), TD = tree density (# trees /800 m²), SD = shrub density (# shrubs /800 m²), DBH 1 = number of individuals in size class 1 (> 10 – 20 cm dbh), DBH 2 = number of individuals in size class 2 (> 20 - 30 cm dbh), DBH 3 = number of individuals in size class 3 (> 30 cm dbh), FHD = foliage height diversity (Shannon –Wiener Index), FHDEN 1 = foliage height density or proportional coverage at > 0 – 2 m, FHDEN 2 = foliage height density at > 2 – 6 m, FHDEN 3 = foliage height density at > 6 – 10 m, HEIGHT = mean tree height (m). NS = No significant differences.

Forests and Regions	Vegetation Structure Variables				
	TBA	TD	SD	DBH1	DBH2
Aquilpo	537.5 ± 53.84 ^b	104.5 ± 12.02	165.0 ± 0.00 ^{ab}	40.5 ± 4.90	15.5 ± 2.12 ^{ab}
Ishinca	340.3 ± 61.85 ^{ab}	91.0 ± 19.79	269.0 ± 11.51 ^{ab}	56.6 ± 12.02	31.5 ± 7.77 ^{abc}
Morococha	175.5 ± 76.57 ^a	70.5 ± 34.64	268.5 ± 45.96 ^{ab}	54.0 ± 31.11	16.0 ± 2.82 ^{ab}
Llanganuco	157.4 ± 18.51 ^a	56.5 ± 6.36	264.5 ± 2.12 ^{ab}	56.6 ± 13.43	39.5 ± 2.12 ^{bc}
C. Blanca	302.7 ± 169.31 ^A	80.6 ± 25.35 ^{AB}	241.7 ± 50.67 ^{AB}	51.8 ± 15.44	25.6 ± 11.57 ^A
Yauí	363.7 ± 12.19 ^{ab}	83.0 ± 2.82	101.0 ± 72.12 ^a	45.5 ± 7.77	33.5 ± 6.36 ^{abc}
Maticuna	59.4 ± 42.09 ^a	42.0 ± 24.04	273.0 ± 147.07 ^{ab}	40.5 ± 23.33	1.5 ± 0.70 ^a
Japani	75.3 ± 10.75 ^a	48.5 ± 3.53	32.5 ± 13.43 ^a	46.0 ± 2.82	2.5 ± 0.70 ^a
Quichas	131.0 ± 19.68 ^a	65.5 ± 6.36	175.5 ± 32.22 ^{ab}	57.0 ± 11.51	8.0 ± 4.24 ^{ab}
C. Occidental	157.3 ± 131.82 ^B	59.7 ± 19.52 ^A	145.5 ± 24.38 ^A	47.2 ± 12.13	11.5 ± 14.21 ^B
Yanacocha	550.4 ± 213.66 ^b	149.0 ± 35.35	463.0 ± 179.60 ^b	82.5 ± 9.19	65.0 ± 25.45 ^c
Sacsamonte	350.6 ± 106.08 ^{ab}	56.0 ± 9.89	160.5 ± 41.71 ^{ab}	25.0 ± 9.89	24.0 ± 4.24 ^{ab}
Pumahuanca	175.7 ± 15.43 ^a	85.5 ± 14.84	189.0 ± 80.61 ^{ab}	72.5 ± 20.50	12.0 ± 4.24 ^{ab}
Quenuamonte	370.0 ± 162.58 ^{ab}	101.5 ± 51.61	251.5 ± 27.57 ^{ab}	67.5 ± 44.54	26.5 ± 9.19 ^{ab}
C. Vilcanota	361.7 ± 177.37 ^A	98.0 ± 43.58 ^B	266.0 ± 148.04 ^B	61.8 ± 30.34	31.8 ± 23.70 ^A
MANOVA Local F _{9,12}	6.03 ^{**}	NS	2.90 [*]	NS	7.90 ^{***}
MANOVA Region F _{2,12}	10.73 ^{**}	5.29 [*]	4.43 [*]	NS	11.70 ^{**}

Forests and Regions	Vegetation Structure Variables					
	DBH 3	FHD	FHDEN1	FHDEN2	FHDEN3	HEIGHT
Aquilpo	0.5 ± 0.70 ^b	1.5 ± 0.15	0.10 ± 0.07 ^a	0.17 ± 0.02 ^a	0.72 ± 0.05 ^{de}	12.9 ± 2.55 ^b
Ishinca	3.0 ± 0.00 ^b	1.5 ± 0.20	0.09 ± 0.02 ^a	0.10 ± 0.09 ^a	0.80 ± 0.07 ^e	7.6 ± 0.11 ^{ab}
Morococha	0.5 ± 0.70 ^b	2.0 ± 0.01	0.33 ± 0.08 ^{ab}	0.42 ± 0.02 ^{abc}	0.24 ± 0.06 ^{abc}	8.4 ± 1.59 ^{ab}
Llanganuco	8.5 ± 3.53 ^a	1.9 ± 0.01	0.34 ± 0.01 ^{ab}	0.47 ± 0.09 ^{abc}	0.18 ± 0.08 ^{ab}	4.4 ± 1.56 ^a
C. Blanca	3.1 ± 3.75	1.7 ± 0.27 ^A	0.21 ± 0.13	0.29 ± 0.17 ^A	0.48 ± 0.30 ^A	8.3 ± 3.48
Yauí	.0 ± 1.51 ^b	1.9 ± 0.04	0.10 ± 0.06 ^a	0.29 ± 0.01 ^{ab}	0.60 ± 0.04 ^{cde}	7.6 ± 0.36 ^{ab}
Maticuna	ND	1.5 ± 0.35	0.56 ± 0.16 ^b	0.42 ± 0.14 ^{abc}	0.01 ± 0.02 ^a	4.5 ± 2.88 ^a
Japani	ND	1.8 ± 0.05	0.23 ± 0.04 ^a	0.71 ± 0.02 ^c	0.05 ± 0.06 ^a	7.3 ± 3.69 ^{ab}
Quichas	0.5 ± 0.70 ^b	1.9 ± 0.02	0.26 ± 0.07 ^{ab}	0.59 ± 0.00 ^{bc}	0.14 ± 0.07 ^{ab}	6.8 ± 0.94 ^{ab}
C. Occidental	1.1 ± 1.88	1.8 ± 0.20 ^{AB}	0.28 ± 0.19	0.50 ± 0.18 ^B	0.20 ± 0.25 ^B	6.6 ± 2.22
Yanacocha	1.5 ± 0.70 ^b	1.9 ± 0.19	0.17 ± 0.08 ^a	0.26 ± 0.12 ^{ab}	0.56 ± 0.20 ^{cde}	7.9 ± 1.24 ^{ab}
Sacsamonte	7.0 ± 4.24 ^b	1.9 ± 0.21	0.16 ± 0.08	0.34 ± 0.22	0.50 ± 0.14 ^{bcd}	8.8 ± 1.75 ^{ab}
Pumahuanca	ND	2.0 ± 0.07	0.30 ± 0.04 ^{ab}	0.45 ± 0.11 ^{abc}	0.25 ± 0.07 ^{abc}	7.0 ± 0.48 ^{ab}
Quenuamonte	4.0 ± 4.24 ^b	2.0 ± 0.01	0.28 ± 0.09 ^{ab}	0.37 ± 0.01 ^{abc}	0.35 ± 0.08 ^{abcd}	7.4 ± 0.53 ^{ab}
C. Vilcanota	3.1 ± 3.64	2.0 ± 0.13 ^B	0.22 ± 0.09	0.35 ± 0.12 ^A	0.41 ± 0.16 ^A	7.8 ± 1.12
MANOVA Local F _{9,12}	4.16*	3.19*	6.18**	4.84**	14.64***	3.00*
MANOVA Region F _{2,12}	NS	4.57*	NS	9.36***	19.23***	NS

Appendix 1.1. Plant families and species present in *Polylepis* woodlands in the study area.

Plant taxonomy classification, nomenclatural authorities, data on endemics (in bold), and elevation range of species follows Bracko and Zarucchi (1993). *WM & GS = W. Mendoza and G. Servat voucher numbers (see text for details). ** *P. weberbauerii* in C. Blanca normally occurs at > 4000 m. NC=Not collected. *** Not included in analysis.

FAMILY	SPECIES	Elevation (m)	Voucher number (WM & GS)*
ASTERACEAE	<i>Ageratina azangaroensis</i> (Schultz-Bip. ex Weddell) K. & H. R.	2000-4500	00191
	<i>Ageratina sternbergiana</i> (DC.) K. & H. R.	500-4500	00009
	<i>Baccharis aff. peruviana</i> Cuatrecasas	3000-4000	00197
	<i>Baccharis buxifolia</i> (Lamarck) Persoon	3000-4000	00014
	<i>Baccharis odorata</i> H.B.K.	3000-3500	00018
	<i>Baccharis phylloides</i> H.B.K.	2000-3500	00192
	<i>Baccharis salicifolia</i> (R. & P.) Persoon	0-3500	00141
	<i>Baccharis latifolia</i> (R. & P.) Persoon	1000-4000	00195
	<i>Bidens andicola</i> H.B.K.	3000-4500	00022
	<i>Diplostephium foliosissimum</i> S.F. Blake	2500-4500	00202
	<i>Gynoxys aff. longifolia</i> Weddell	3500-4000	00027
	<i>Gynoxys aff. nitida</i> Muschler	3000-4500	00025
	<i>Gynoxys aff. visoensis</i> Cuatrecasas	2500-3500	00163
	<i>Gynoxys caracensis</i> Muschler	2500-4500	00208
	<i>Gynoxys macfrancisii</i> Cuatrecasas	2500-3000	00207
	<i>Gynoxys pillahuatensis</i> Cuatrecasas	3000-3500	00028

FAMILY	SPECIES	Elevation (m)	Record number (WM & GS)*
	<i>Loricaria ferruginea</i> (R. & P.) Weddell	3000-4500	00161
	<i>Mutisia cochabambensis</i> Hieronymus	3000-4000	00211
	<i>Senecio torrebuasensis</i> Cuatrecasas	4000-4500	00034
	<i>Senecio hobenackeri</i> Schultz-Bip.	3000-4500	00046
	<i>Senecio usgarens</i> Cuatrecasas	2500-3500	00196
	<i>Senecio</i> sp	---	00150
BERBERIDACEAE	<i>Berberis carinata</i> Lechler	3000-3500	00056
	<i>Berberis humbertiana</i> J.F. Macbride	3000-3500	00053
CARYOPHYLLACEAE	<i>Arenaria lanuginosa</i> (Michaux) Rohrbach	1000-4500	00058
ERICACEAE	<i>Pernettya prostrata</i> (Cavanilles) Sleumer	2000-4500	00066
FABACEAE	<i>Lupinus</i> sp	---	00239
GENTIANACEAE	<i>Gentianella sandiensis</i> (Gilg) J. Pringle	3000-4000	00072
SAXIFRAGACEAE	<i>Escallonia myrtilloides</i> L.	2500-4000	00083
	<i>Ribes brachybotrys</i> (Weddell) Janczowski	2500-4500	00080
LAMIACEAE	<i>Minthostachys mollis</i> Grisebach	500-3500	00247
	<i>Satureja boliviana</i> (Benth) Briquet	3000-4500	00085
LILIACEAE	<i>Bomarea dulcis</i> (Hooker) Beauverd	3000-4500	00002

FAMILY	SPECIES	Elevation (m)	Record number (WM & GS)*
LOGANIACEAE	<i>Buddleja aff. montana</i> Britton	2500-4000	00225
MELASTOMATACEAE	<i>Brachyotum naudinii</i> Triana	2500-4000	00263
PIPERACEAE	<i>Peperomia hartwegiana</i> Miquel	3000-4500	00272
POACEAE***	<i>Stipa ichu</i> (R. & P.) Kunth	1000-4500	NC
	<i>Festuca dolichophylla</i> J. S. Presl	3500-4500	NC
	<i>Calamagrostis rigescens</i> (J. S. Presl) Scribner	3500-4500	NC
POLYGALACEAE	<i>Monnina salicifolia</i> R. & P.	1500-4500	00104
POLYGONACEAE	<i>Muehlenbeckia nummularia</i> H. Gross	3000-4000	00274
	<i>Rumex acetocella</i> L.	2000-4500	00273
ROSACEAE	<i>Polylepis racemosa</i> R. & P.	3000-4500	00172
	<i>Polylepis incana</i> H. B. K.	2500-4500	00358
	<i>Polylepis sericea</i> Weddell	2500-4500	00277
	<i>Polylepis weberbauerii</i> Pilger	2000-4500*	00171
SCROPHULARIACEAE	<i>Bartsia bartsoides</i> (Hooker) Edwin	2000-4500	00119
	<i>Calceolaria engleriana</i> Kraenzlin	2000-4500	00127
SOLANACEAE***	<i>Salpichroa hirsuta</i> (Meyen) Miers	3000-4500	NC
URTICACEAE	<i>Urtica echinata</i> Bentham	3500-4500	00178

FAMILY	SPECIES	Elevation (m)	Record number (WM & GS)*
VERBENACEAE	<i>Duranta mandonii</i> Moldenke	2500-4000	NC
PTERIDOPHYTES	<i>Adiantum poerettii</i> Wikstrom	---	NC
	<i>Melpomene flobelliformis</i> (Poiret) A. R. Sm & R. C. Moran	---	00329
	<i>Asplenium haenkeanum</i> (C. Presl) Hieron.	---	00333
	<i>Asplenium castaneum</i> Schlecht & Cham	---	00337

CHAPTER TWO

INTRASPECIFIC VARIATION IN THE FORAGING NICHE OF BIRDS ASSOCIATED WITH *POLYLEPIS* WOODLANDS: THE INFLUENCE OF LOCAL AND REGIONAL FACTORS

The niche concept has played a central role in ecology for nearly a hundred years, mainly to gain insights into community organization (Gause 1930, Hutchinson, 1957, MacArthur 1958, 1965, Connell 1951, MacArthur and Levins 1964, MacArthur and Pianka 1966, Emlen 1966, Levin 1970, Tilman 1982, for a review see Chase and Leibold 2003). Contemporary theory defines the niche of a species as the requirements for existence in a given environment (*i.e.*, the n-dimensional hyper-volume niche, Hutchinson 1957) and its role on that environment (Ricklefs 1997, Chase and Leibold 2003, Naeem 2003), extending the “Principle of Competitive Exclusion” (Gause 1930, Hardin 1960) to the condition that only species with sufficiently differentiated niches may coexist within the same community or environment (for review see Futuyma and Moreno 1988, Chase and Leibold 2003).

Classic niche studies have focused on resource-based, interspecific differences based on competition theory to determine how two or more species with similar niches can coexist by partitioning habitats (*e.g.*, *Paramecium*, Gause 1930; grain beetles, Crombie 1945-1947, Park 1948), microhabitats (*e.g.*, barnacles, Connell 1951; *Dendroica* warblers, MacArthur 1958), resources (*e.g.*, algae and terrestrial plants, Tilman 1976, 1982), and foraging heights (*e.g.*, warblers, MacArthur 1972). Based on these studies, interspecific differences in niche partitioning were inferred to influence the ecological outcomes of communities (see review in Chase and Leibold 2003, but see Hubbell 2001). However, communities include

conspecifics as well as other species, and intraspecific differences in the niche also have ecological and evolutionary consequences for the species and communities involved (Van Valen 1965; Grant 1967, 1979; Roughgarden 1972, 1974; Bolnick *et al.*, 2003). Moreover, as natural selection operates at the level of the individual, the importance of including measures of intraspecific variation in species' niche has been seen with renewed interest in studies of local adaptation, adaptive radiation, and ecological speciation (*e.g.*, Losos 1990, Throwbridge 1991; Dayan and Simberloff 1994, Linhart and Grant 1996, Reznick and Travis 1996, Nagy and Rice 1997, Bronikowski 2000, Olson and Uller 2003, Bolnick *et al.* 2003, Scott *et al.* 2003, Meiri *et al.* 2005).

Intraspecific variation in the niche is likely affected by local differences in abiotic and biotic factors (*e.g.*, temperature, Houlihan *et al.* 2000; Shuter *et al.* 1980; Magnusson *et al.* 1979; elevation, Berven 1982, 1990; microclimate, Martin 1998, 2001; habitat diversification, Robinson and Wilson 1994; prey distribution, Ehlinger and Wilson 1988; intraspecific competition, Smith 1990; predation, Martin 1993, 1998, Gilliam and Fraser 2001, Werner 1984). Furthermore, the niche may also be influenced by a complex and dynamic set of past and present factors acting on different spatial and temporal scales as shown in a variety of studies across taxa (*e.g.*, Darwin's finches, Grant 1986; Caribbean *Anolis* lizards, Losos 1990, Losos *et al.* 1998, 2003; stream fishes, Angermeier and Winston 1998; desert rodents, Kelt 1999; plants in calcareous grasslands, Pärtel and Zobel 1999).

Quantitative approaches to the study of interspecific and intraspecific niche variation are based on measures of its components (Roughgarden 1972, 1974, Bolnick *et al.* 2003): breadth and plasticity. Niche breadth is defined as the number of resources used by a particular species and measures if the species is a specialist or generalist relative to other

community members or species in a clade (Futuyma and Moreno 1988, Mac Nally 1995 and references therein). A specialist uses a relatively limited fraction of the range of available resources (i.e., narrow niche breadth, Fig. 2.1 A) while a generalist uses a relatively large fraction of the resources available (i.e., broader niche breadth, Fig. 2.1 A) without regard for underlying mechanisms that determine how the species manages to identify, select, and capture a particular resource or the fitness effects on the focal species (Bolnick 2003; *e.g.*, Sherry 1984, Mac Nally 1995). Niche plasticity evaluates how restricted or plastic is the niche of a species within and across populations (Fig. 2.1 B) (Mac Nally 1995, Roughgarden 1972, 1974; Bolnick *et al.*, 2003). The term restricted applies to the conditions under which intraspecific regularities in the niche might be maintained, and the term plastic applies when niche regularities within and across populations break down (Sherry 1990, Price 1991, Price and Jamdar 1991, Richman and Price 1992, Holbrook and Schmitt 1992, Forstmeier *et al.* 2001). Thus, a species may have a restricted (or plastic) niche, even if its niche breadth is narrow (specialist) or wide (generalist) provided if it remains consistent across populations throughout its distribution (*i.e.*, restricted populations may be made up of individual generalists or, equally plausibly, from a variety of individual specialists) (Fig. 2.1 C). Both components provide complementary information for comparisons at different spatial scales and levels of organization (*e.g.*, populations, species, and communities).

In this study, I examined intraspecific niche variation (or lack thereof) of nine species of forest interior, arboreal, arthropod-feeding birds (hereafter, insectivorous) of the *Polylepis* (Rosaceae) community, a high elevation system of the Andes. I focus the study from a behavioral perspective because foraging behavior (along with physiology and morphology) is crucial to adapt to new habitats and, it is an important target of selection

(*e.g.*, Sherry 1985, 1990, Morimoto and Wasseman 1991, Losos 1990). In addition, at high elevation systems, arboreal-insectivorous birds spend most of their time and effort using several substrates and maneuvers to search and obtain food, so it is likely that the way in which individuals forage influences their performance, as natural selection should favor those strategies that maximize fitness or some proxy of fitness (*e.g.*, rate of resource acquisition, production of offspring). Specifically, I quantify the niche breadth and plasticity based on measures of a) microhabitat use (Levin's index), and b) foraging categories used (measured by plotting maneuvers and substrates in multivariate space, *cf.* Mac Nally 1995). Measures of variation in breadth and plasticity were analyzed in light of variation in ecological factors across *Polylepis* woodlands. I focus on three factors that may vary locally: food resources, floristic composition, and vegetation structure because these have been reported to influence the niche of species intra and interspecifically (Wiens 1989, Werner and Sherry's 1987, Lewontin 1987, Cadle and Greene 1993, Cornell and Lawton 1992, Latham and Ricklefs 1993, Francis and Currie 1998, Huston 1999). Fluctuations in the relative abundance, availability of alternative food types, spatial relationship among resources, attributes of resources such as palatability and/or hardness have been reported to influence: a) the relative abundance of individuals in populations or communities; b) seasonal migration (*e.g.*, Rabenold 1978, 1979, 1980, Recher *et al.* 1983, 1985, Recher and Holmes 1985, Loiselle and Blake 1991, Blake and Loiselle 1991); c) opportunistic aggregation in areas of high food abundance (*e.g.*, Brush and Stiles 1986); and d) partition of food resources (*e.g.*, Holmes and Shultz 1988, Holmes and Pitelka 1968), foraging substrates (*e.g.*, Hejl and Verner 1990), and strata. Besides food resources, variation in floristic composition is expected to provide a set of opportunities and constraints that may result in

close associations between birds and particular plant species. In addition, variation in plant species composition could affect foraging ecology of birds because of differences in the spatial arrangement of leaves, branching patterns, and other parameters of plant species' architecture (*e.g.*, Holmes and Robinson 1981, Franzeb 1983, Morrison *et al.* 1985, Tomoff 1974, James and Wamer 1982, Rotenberry 1985, Wiens and Rotenberry 1981, MacNally 1990, 1995). Vegetation structure in forests with high diversity of plant species may also be more complex in terms of strata (*i.e.*, number of layers in understory, subcanopy, and canopy) and life forms (*i.e.*, shrubs, small trees, large trees) and, thus, provide more substrates or microhabitats in which to forage when compared to low diversity woodlands (Holmes *et al.* 1979, Robinson 1981, Robinson and Holmes 1984). Some characteristics of habitat structure known to affect foraging ecology of birds are the number or types of substrates available (Jackson 1979, Fitzpatrick 1980, Greenberg and Gradwohl 1980) and forest physiognomy (Robinson and Holmes 1984, Whelan 1989, in Mac Nally 1995, Maurer and Whitmore 1981, Sabo and Holmes 1983). Moreover, regional factors, such as biogeography (*i.e.*, the presence of barriers that have an effect on species dispersal), may influence the niche of a species within and across populations (*e.g.*, Wiens 1989, Werner and Sherry's 1987, Lewontin 1987, Cadle and Greene 1993, Cornell and Lawton 1992, Latham and Ricklefs 1993, Francis and Currie 1998, Huston 1999). The relative importance of regional factors (*i.e.*, biogeography) in explaining foraging niche variation is indirectly assessed in this study by selecting a series of *Polylepis* woodlands nested within three distinct biogeographic regions of the Peruvian Andes.

The goals of the present study are 1) to measure the extent of variation in two foraging niche components (breadth and plasticity) of nine species of arboreal-insectivorous

birds in light of local conditions (*e.g.*, food resources availability, floristic composition, and vegetation structure) in a series of *Polylepis* woodlands nested within three distinct biogeographic regions, and 2) determine the relative importance of local and/or regional factors in explaining niche patterns.

The hypotheses of the study are: 1) Variation in local and/or regional factors within and across woodlands influences intraspecific measures of the foraging niche (breadth and plasticity) of birds associated with the *Polylepis* community (“local/regional factors hypothesis”). Support for the hypothesis could result in two non-mutually exclusive scenarios: a) If the foraging niche varies in response to local factors, niche breadth and plasticity will track one or more local factors (*i.e.*, abundance of food resources, floristic composition or vegetation structure); b) If niche varies regionally, I expect differences in species niche breadth and plasticity across regions but not among forests within region. 2) Intraspecific measures of foraging niche of birds are static and do not reflect variation in local or regional factors within or across *Polylepis* woodlands (“historical/morphological factors hypothesis”). If foraging niche breadth and plasticity of bird species do not vary within and across populations, despite variation in local and regional factors, history of taxa and/or morphology likely constrains the foraging niche of the species.

METHODS

Study system

Throughout the high Andes from 3400 to 4600 m, *Polylepis* woodlands are typically found close to streams or as small patches in canyon gorges on slopes and cliff-edges; these

forests in Peru are surrounded by Puna grasslands. The *Polylepis* community is dominated by *Polylepis* (Rosaceae) trees and characterized by high levels of endemism in flora and fauna and thus, it is of great interest from evolutionary and ecological perspectives (Fjeldså and Krabbe 1990, Fjeldså 1992a, b, c; 1993). *Polylepis* woodlands are scattered in different biogeographic regions throughout the Andes, offering discrete units of study (*i.e.*, local communities) within a historical framework. Moreover, the flora and fauna are relatively simple when compared to more species-rich woodlands at lower elevations, allowing comprehensive studies at different scales (local, regional) and levels of organization (species, populations, communities).

The patchy occurrence of *Polylepis* woodlands is attributed to microclimatic and physiological requirements (Weberbauer 1945, Troll 1959, 1968, Koepcke 1961, Walter and Medina 1969, Simpson 1979, 1986, Vuilleumier 1984, Rauh 1988). Yet it also has been suggested that these woodlands are relicts of a once more widespread habitat during the Pleistocene (*i.e.*, 10,000-20,000 years ago) (Ellenberg 1958, Beck and Garcia 1991, Fjeldså 1992a, Hensen 1993, Kessler 1995).

Regional settings

The present study was conducted in three separate regions of the Peruvian Andes: Cordillera Blanca, C. Occidental, and C. Vilcanota (Fig. 2.1), areas that have been proposed as distinct glacial Pleistocene refuges for a number of taxa (Fjeldså 1992a, 1993, Fjeldså and Kessler 1996) and as different biogeographic regions (Berry 1982, Koepcke W. 1961, Koepcke M. 1961, Lamas 1982, Fjeldså 1992 a, Simpson 1975, Smith 1988). In more humid regions *Polylepis* woodlands often have some dense, shady sections with deep fertile soil and

lush vegetation of herbs between moss-covered rocks. Trees are heavily laden with mosses, vines (e.g., *Bomarea*, *Mutisia*, *Passiflora*, and *Salpicbroa*) and mistletoes (i.e., *Tristerix*); bushes and trees of *Gynoxys* (Asteraceae) are often interspersed with *Polylepis*.

Very few climatic data are available for the study regions, but high Andean systems are generally characterized by small annual variation in mean temperature while daily patterns may go from freezing temperatures during the night (-3 ° C) to high daytime temperatures (24° C) (Sarmiento 1986). Precipitation in tropical mountains occurs when the Inter-tropical Convergence Zone (ITCZ) is at its southernmost point (40°- 45° latitude south). Variation in the position of the ITCZ drastically affects rainfall in the mountains resulting in the wet (December - April) and dry seasons (May - November). However, precipitation patterns during the wet season tend to be more complex and variable within regions than across regions due to exposure to winds and orography (Lenters and Cook 1995).

Local settings

For this study, I selected four *Polylepis* woodlands within each of the three regions that matched the following criteria: 1) sites were above 3500 m where *Polylepis* forms distinct woodlands surrounded by Puna vegetation (Lamas 1982, Kessler 1995); and, 2) woodlands were presumably large enough (> 50 ha) to maintain populations of selected bird species. The woodlands selected for the present study ranged in size from 50 - 300 ha (Table 2.1); and the dominant *Polylepis* species occurring in each forest were: 1) C. Blanca: Aquilpo and Ishinca (*P. weberbauerii*), Morococha and Llanganuco (*P. sericea*); 2) C. Occidental: Yauí and

Quichas (*P. weberbauerii*); Maticuna and Japani (*P. incana*); and 3) C. Vilcanota: Yanacochoa, Sacsamonte, Pumahuanca, Quenuamonte (*P. racemosa*).

General study design

I collected data in 12 *Polylepis* woodlands from May - December 1997 (foraging niche of birds, floristic composition, and vegetation structure) and returned to the same woodlands in May - October 1998 (foraging niche of birds, arthropod resources) (Table 2.1) which corresponded to the dry season and beginning of the rainy season. In all cases, I used a hierarchical sampling design with the four woodlands nested within each of three regions. In each *Polylepis* forest, I collected data on foraging niche of birds and abundance of arthropod resources in two sets of four 100 x 10 m transects placed 50 m apart from each other. The last transect from the first set was separated by at least 500 m from the first transect of the second set (hereafter the two sets of transects will be referred as plots). I took data on floristic composition and vegetation structure in two 20 x 5 m belts embedded within each transect. To examine variation in local factors such as arthropod abundance, floristic composition and vegetation structure among woodlands, I used plots within woodlands as replicate units (Chapter I).

Study birds

Approximately 112 bird species are regularly found in *Polylepis* woodlands of the Andes of Peru. This number includes opportunistic visitors from lower montane forests and surrounding grasslands, bogs, and wetlands (Fjeldså 1992 a, 1997). Of these 112 species, at least 22 are found in *Polylepis* woodlands as regular breeding residents (= associated

species) (Fjeldså and Krabbe 1990, Fjeldså 1992 a, b, c, 1993). I studied nine species of forest-interior, arboreal, insectivorous birds associated with the community: *Oreomanes fraseri*, *Cranioleuca baroni* (or its ecological replacement *C. albicapilla*), *Xenodacnis parina*, *Leptasthenura pileata* (or its ecological replacement *L. xenothorax*), *L. yanacensis*, *Mecocerculus leucophrys*, and *Octhoeca rufipectoralis* (Table 2.2) (cf. Fjeldså and Krabbe 1990, Fjeldså 1992 a, b, c).

I made observations of actively foraging birds using the Remsen and Robinson (1990) classification of foraging behavior. I quantified microhabitats, defined here as parts of the habitat where individuals forage, which in this case, are given by the combination of plant species and substrate used by birds (*e.g.*, *Polylepis* bark, *Gynoxys* foliage), and maneuvers (prey capture attempts, *e.g.*, glean, probe) used by individual birds. At each forest, I made observations throughout the day, most of which occur between 0800-1200 hrs, and 1400-1700 hrs, for four and six consecutive days in 1997 and 1998, respectively. I systematically walked transects and moved from one foraging bird to another using focal-animal sampling (Altmann 1974); observations of foraging birds were audio-recorded, or videotaped when possible. I obtained foraging observations (*i.e.*, maneuvers and microhabitats used) from a minimum of 10 individuals of each species in each of the 12 *Polylepis* woodlands. For each individual, the average length of continuous foraging time recorded was 180 seconds (individuals observed less than 180 seconds were excluded from analysis), which was later divided into 60-second sequences. As the number of continuous observations obtained for each species was highly variable in each *Polylepis* forest. I first chose 20 individuals and randomly selected one 60-second sequence from each continuous observation. This procedure allowed me to lessen biases that may exist due to lack of independence of observations (*i.e.*, foraging maneuvers and microhabitat use may depend on previous

behaviors). For a few sites, however, this was not possible because of small sample size, in which case I used all sequences collected. I combined foraging maneuvers and microhabitats for each sequence into categories (Fig. 2.2). Some rare foraging combinations (those used 1 or 2 times in only one of the 12 localities) were excluded from analyses.

The main data set consisted of columns that represented 25 foraging categories and 1480 rows corresponding to each individual/species/forest (1480 rows instead of 1600 due to the absence of species at some sites). Counts of the total number of times that each foraging category was used by each individual in the 60-second sequence (hereafter = individuals) fill the cells of the matrix. From these data, I constructed different matrices for analyses.

Variation in local factors

I measured local food availability (i.e., types and abundance of arthropods in different microhabitats), floristic composition (i.e., plant species richness and abundance), and horizontal and vertical vegetation structure, as factors that can shape the foraging niche of birds.

Food resources. - Food resources may affect how birds move through the habitat and how they encounter and capture prey. To measure the abundance of arthropods, the primary food resource of study birds, I identified microhabitats (i.e., “patches” containing food resources that can be discriminated by an individual; Morris 1987 in Mac Nally 1995) as the unit of sample. Microhabitats were defined by the combination of dominant plant species (i.e., *Polylepis*, *Gynoxys*, *Tristerix*) and substrates used (i.e., bark, foliage), except for the moss attached to the branches of *Polylepis* trees (that included many epiphytic species). I

quantified arthropods by focusing on discrete microhabitats used by foraging birds (based on preliminary studies): *Polylepis* bark; *Polylepis*, *Gynoxys*, and *Tristerix* foliage; and moss. Due to the structural differences among microhabitats, arthropod sampling varied. I sampled arthropods from the trunk of *Polylepis* trees by removing a 20 x 20 cm quad, 150 cm above the ground. *Polylepis*, *Gynoxys*, and *Tristerix* foliage (twigs with leaves) were sampled by clipping three or four 30-cm terminal twigs selected randomly from the lower to middle crown of trees or shrubs. To sample arthropods from moss, I removed a 20 x 20 cm quad of moss from branches (150 cm from the ground). In every case, I sampled 24 *Polylepis* trees (or *Gynoxys* shrubs or trees and *Tristerix* plants) equally divided between the two plots and calculated arthropod abundance per microhabitat across *Polylepis* woodlands. Samples of bark, foliage, and moss were placed in plastic bags and weighed using a “Pesola” scale. In all cases, attempts were made to sample similar amounts of bark, moss, and foliage per sample (ca. 50 gm). Arthropods were removed using tweezers, counted and preserved in 70 % alcohol. Arthropods with aposematic coloration, low occurrence (< 5 individuals per microhabitat), or less than 2 mm length, were excluded from the present study as they likely do not constitute prey for birds due to low acceptability or detectability (Wolda 1990, Servat 1995).

Floristic richness and composition.- Plant species richness and composition at each *Polylepis* forest was measured by counting and identifying trees (>10 cm dbh) and “woody stems” (<10 cm dbh) found in the forest interior (*i.e.*, 50 m away from edge of the plot, see study design above). The data obtained were used to build a matrix consisting of 12 *Polylepis* woodlands (rows) by 50 plant species (columns), cells were filled with the total number of individuals found.

Vegetation structure.- I divided vegetation structure variables into those that represent “horizontal complexity” (*i.e.*, the distribution of tree size classes, density of vegetation, and tree diameter) and those that represent the “vertical complexity” of the habitat (*i.e.*, the diversity of vegetation heights and density of foliage at those heights, vertical layers: understory, subcanopy and canopy) (*e.g.*, MacArthur et al. 1962, Robinson and Holmes 1984, Rotenberry 1985, MacNally 1990, 1995).

1. Vertical structural variables

a. *Mean tree height (HEIGHT).*- I measured trees using a telemetric graduated pole (12 m, Hastings Telescoping Measuring Rod).

b. *Foliage height density (FHDEN).*- I took measurements of foliage height density, with a telemetric graduated pole, along "vertical" transects every 20 m along the two sets of 100 m transects (see study design). The number of times vegetation “intersected” the pole in a radius of 25 cm was recorded at the following intervals: 0-2 m (*FHDEN1*), > 2-6 m (*FHDEN2*), and > 6-10 m (*FHDEN3*). Vegetation contacts were summed within each interval across points and then divided by total contacts across all heights to obtain a proportion of foliage density occurring within different heights.

2. Horizontal structural variables

a. *Tree size classes (DBH).*- I measured diameter at breast height for each tree encountered, regardless of species identity, and assigned them to one of three size categories: > 10-20 m dbh (*DBH1*), > 20-30 m dbh (*DBH2*), and > 30 cm dbh (*DBH3*). For each local factor, I used data obtained in plots as replicates in the models. All variables were tested for normality, and equality of variances.

b. Total basal area (TBA).- Total basal area was measured to describe tree coverage.

TBA was calculated by converting measures of dbh (*i.e.*, distance at breast height) to circular area, estimating proportional basal area for each tree species and adding all tree basal areas for each plot.

c. Tree (TD) and shrub density (SD).- I measured tree and shrub density by counting the number of trees (> 10 cm dbh) or woody stems (> 50 cm height and < 10 cm dbh) per plot and dividing the total by the sampled area to obtain density values.

Regional factors.- Regional factors in this study refer to history of the environment (*i.e.*, biogeography) and are inferred by the study design in which four independent *Polylepis* woodlands were nested within each biogeographic region.

Data analysis

To determine if foraging niche of each of the focal species vary across and within populations, I measured breadth and plasticity.

Niche breadth.- The niche breadth is a measure of variability in the extent to which a species uses resources (Feinsinger et al. 1981, Gotelli and Graves 1996). In this study, measures of breadth indicated the degree to which microhabitat exploitation was evenly spread among alternative states. I used Levin's non-conformance niche breadth (Levins 1968) given by: $1 / \sum_i (p_i)^2$ where p_i is the proportion of resource items (microhabitats) in state i out of all items used by the population. For each species, low values of niche breadth imply that a small number of potential microhabitats were used (*i.e.*, specialist) across populations, whereas relatively high values indicated a large number of microhabitats were

used more evenly (*i.e.*, generalist). It is important to note that values of niche breadth were not absolute, but relative values across species and populations.

To analyze niche breadth, I selected one species at a time and calculated the niche breadth, based on the foraging microhabitats used by each individual in a population (replicates). I compared variation in niche breadth values (dependent variable) across *Polylepis* woodlands and regions of the Andes (as the main effect and nested factors respectively) using Hierarchical Multivariate Analysis of Variance (*SPSS*, Version 10) to separate out the variation attributed to regional (*i.e.*, among regions), or local niche breadth (*i.e.*, among woodlands within regions) by levels of significance. I followed the analysis with Post-hoc Tukey (HSD) test when appropriate. Based on statistical significance of niche breadth, and the observed mean (and SD), I categorized species into specialists (if mean niche breadth was relatively narrow, variation is small and no significant differences are detected across woodlands and regions), or generalist (if mean niche breadth was relatively broad, highly variable and significant differences were found across woodlands and regions of study).

Niche plasticity.- Plasticity is a measure of the foraging niche consistency within and across populations of the same species. Thus, species could be restricted if intraspecific regularities in the niche are maintained, or plastic if niche regularities within and across populations break down. In this study, bird species may have a restricted (or plastic) niche, even if its niche breadth is narrow (specialist) or wide (generalist) as long as it remains regular across populations (*i.e.*, restricted populations may be made up of individual generalists or, equally plausibly, from a variety of individual specialists) (Fig. 2.1 C).

I determined foraging plasticity for each bird species across *Polylepis* woodlands and regions by identifying the “spatial position” that each individual occupies in the population. I employed *PC-ORD* Version 4 (McCune and Mefford 1999) to do Bray Curtis ordination. I selected Sorensen’s percent dissimilarity as a measure of distance between points (individual birds). This index is commonly used with ecological data because it retains sensitivity in heterogeneous data sets and gives less weight to outliers (McCune and Mefford 1999). I used the variance regression method for end point selection and Euclidean distance for axis projection geometry (Beals 1984, Greig-Smith 1983, McCune and Mefford 1999). The arrangement of points (*i.e.*, each individual position along the first two axes) obtained from the ordination represents the linear combinations of all foraging categories used by within and across populations. Thus, I selected one bird species at a time, and for each population, I used the scores of all individuals along the first two axes from the previous ordination (see above) to calculate the population centroid. To obtain a single value for the two-dimensional position of each individual, I used the algebraic expression $a^2 + b^2 = c^2$; where a is the difference between the location of the centroid and the location along the first axis of each individual within the population, b is the difference between the location of the centroid, and the location along the second axis of individuals in the population, and consequently c represents the distance to the centroid. For each population, I calculated the mean c value and the standard deviation; or the square root of the sum of the position divided by the number of observations minus one [$SD = \sqrt{\sum c^2 / (n-1)}$] to represent niche plasticity.

To analyze data I used the c value (dependent variable) of individuals in each population as replicates in Hierarchical Multivariate Analysis of Variance (*SPSS*, Version 10)

to separate out the variation attributed to the main effect (*i.e.*, among regions of the Andes), or nested factor (*i.e.*, among woodlands within regions) by levels of significance. I followed the analysis with Post-hoc Tukey test when appropriate.

Variation in ecological factors

To determine if food resources, floristic composition richness, and vegetation structure vary locally and/or regionally I first analyzed each factor independently.

Food resources and floristic composition.- I used rarefaction to analyze variation in richness of food resources (arthropods/microhabitat) and plants using plots as replicates across *Polylepis* woodlands. Rarefaction uses probability theory to derive the expected mean and variance of species richness for a sample of a given size (Hurlbert 1971, Heck et al. 1975, Gotelli and Graves 1996). I used *Ecosim* (Gotelli and Entsminger 2004) to obtain the expected mean richness and variance (of plants and arthropods, independently) while controlling for the number of individuals (Sanders 1968 in Gotelli and Graves 1996). The process was simulated 1000 times specifying the number of individuals that are randomly drawn from each sample.

Vegetation structure.- To analyze variation in vegetation structure within and across *Polylepis* woodlands, I used the mean and SD for each of the 11 variables measured (plots as replicates). Local and/or regional variation in food resources, floristic composition, and vegetation structure were tested using hierarchical *MANOVA* models to interpret foraging niches. As before, hierarchical *MANOVA* tests separated out the variation attributed to regional (*i.e.*, among regions) or local scales (*i.e.*, among woodlands within regions) by levels of significance.

After the independent analyses of local factors, I determined the relative importance of local and regional factors in the foraging niche of birds. I used *Mantel* Tests (*Mantel* 1967, Sokal and Rohlf 1995, Burgman 1987) to identify the relative effect of local and regional factors in explaining patterns of foraging niche of each bird species across woodlands. I used seven independent models (one for each bird species) and built distance matrices to obtain a measure of resemblance (= Sorensen's dissimilarity index) in foraging niche for each possible pair of populations (response variable), and a measure of resemblance in food resources, floristic composition, vegetation structure, region, and geographic distance (predictor variables) for each possible pair of sites. *Mantel* test uses a regression approach to evaluate the null hypothesis of no relationship between two distance matrices and basically determined if pair-wise population differences in foraging categories could be explained by pair-wise differences in any of the factors measured. I customized distance matrices for each bird species, since some of the variables measured (*i.e.*, food resources) were used differently by different bird species. Each model consisted of the following distance matrices:

a. Foraging matrix.- To evaluate the relationship between site similarities in food resources used and foraging behavior of species I selected one species at a time from the main data matrix (see above), and summed up all counts for each foraging category used across all individuals within a population. This resulted in a matrix of 7-12 populations (based on the presence of the species at a site) x 6-11 foraging categories (11 was the maximum number of categories used by any one species from the total 25).

b. Food resources matrix.- The relationship between similarities in food resources used and foraging behavior of species was evaluated using the total number of arthropods (corrected by weight of bark, foliage, and moss) to build a forest x microhabitat matrix (7-12

sites x 3-5 microhabitats used). Data on food resources were customized for each bird species based on which foraging microhabitat(s) used, or if these were present at a site. For instance, in the *Cramiolenca* species I only included data on arthropod abundance from bark and foliage (as this species uses these microhabitats to feed) from localities where the species occurred. Customized matrices for *O. fraseri* included only abundance of arthropods found in bark, while for *Leptasthenura* species I used arthropod data from foliage and bark microhabitats, and for *X. parina* I used *Polylepis*, *Gynoxys* and *Tristerix* foliage. For the two flycatchers, *M. leucophrys* and *O. rufipectoralis*, I used arthropod abundance from *Polylepis* foliage because these likely constitute most of the flying prey caught by the birds during aerial maneuvers.

c. Floristic composition matrix.- To evaluate the relationship between site similarities in floristic composition and bird species foraging behavior, I built a forest x plant species matrix (12 sites x 50 plant species) in which the presence (“1”) or absence (“0”) of each plant species filled the cells of the matrix.

d. Vegetation structure matrix.- To evaluate the relationship between vegetation structure and foraging niche of birds, I built a forest x vertical structure variables matrix (12 sites x 4 variables) and a forest x horizontal structure variables matrix (12 sites x 5 variables) in which a single measure for each variable (averaging data from the two plots, see study design) filled the cells of the matrix.

e. Region matrix.- A “regional distance matrix” was built by examining each forest pair and scoring “0” if they belonged to the same region and “1” if they differed (Sokal and Rohlf 1995); this regional variable was added as another predictor in the *Mantel* test.

Distance matrices of predictor variables matched the size of the bird matrix; that is, data on arthropod abundance, floristic composition, vegetation structure, and region were not included at sites where bird species were absent. Except for the “regional distance matrix”, I relativized original matrices by “the norm” (Greig and Smith 1983) using rows or columns to make categories comparable for each population or site; and used Sorensen’s percent dissimilarity as a measure of distance between points (populations or sites).

The models were run using *Permute!* version 3.4, alpha 9 (Legendre et al. 1994), a special version of *Mantel* test, that allows for several predictor variables to be tested over one response variable generating partial regression coefficients and the associated permutation probability for each variable. I used stepwise regression, a backward elimination procedure, and performed 999 permutations of the original matrix to determine the significance probability of the observed relationship among the response and predictor variables.

RESULTS

Proportional use of foraging categories

Insectivorous birds associated with *Polylepis* woodlands differed in the relative proportion of maneuvers and microhabitats used across sites and regions (Fig. 2.3 a-g). Some species, for instance, *O. fraseri*, foraged proportionally more (> 60 %) on the bark of *Polylepis* trees, using to a lesser extent other microhabitats (Fig. 2.3 a). Maneuvers used by *O. fraseri* included several hanging postures (up, down, sideways, upside down) to probe inside the multi-layered bark, or to glean arthropods from the surface. Other bark-foragers such as *C. baroni* (in C. Blanca and C. Occidental) and *C. albicapilla* (in C. Vilcanota) used

proportionally more *Pohlylepis* bark, but also included regularly other microhabitats such as dead branches hanging in the understory or attached to trees, tree surfaces covered by moss, and *Pohlylepis* foliage (Fig. 2.3 b). Comparatively, *Craniolenca* species use more surface gleaning (hover-glean, sally-glean, and reach-glean) than *O. fraseri* (Fig. 2.3 a, b).

More than 80 % of observations of *L. pileata* and its ecological replacement *L. xenothorax* were foraging in *Pohlylepis* foliage (Fig. 2.3 c). The two species used many hanging postures to glean prey from the surface of twigs and leaflets of *Pohlylepis* trees, but interspecific differences were also observed. For instance, at some woodlands *L. pileata* foraged more in shrubs in the understory than *L. xenothorax* (e.g., 30 % in Quichas, Fig. 2.3 c), while *L. xenothorax* used relatively more *Pohlylepis* bark surfaces than *L. pileata* (e.g., 25 % in Sacsamonte and Pumahuanca, Fig. 2.3 c). Moreover, the proportional use of microhabitats varied across populations as well (Fig. 2.3 c). The third *Leptasthenura* species, *L. yanacensis*, differed from the other two in the use of several foraging microhabitats (i.e., dead branches, *Pohlylepis* and *Gynoxys* foliage, moss, *Pohlylepis* bark, shrubs, and ground, Fig. 2.3 d). A similar pattern was observed in the other foliage gleaner, *X. parina*, that used a variety of microhabitats for foraging (*Gynoxys*, *Pohlylepis*, and *Tristerix* foliage) (Fig. 2.3 e).

Species that capture flying insects either flycatching or hover-gleaning such as *M. leucophrys* could vary in the proportional use of foraging categories and strata (i.e., understory, canopy) used across woodlands. For instance in Aquilpo and Llanganuco, *M. leucophrys* flycatch or hover-gleaned relatively more often on prey on the surface of shrubs and *Pohlylepis* foliage, while in the remaining sites *M. leucophrys* was mostly observed flycatching in the canopy (Fig. 2.3 f). The other flycatcher, *O. rufipectoralis*, used relatively more sally-sit and

flycatching to catch flying insects swarming in the air or on the surface of shrubs in the understory (Fig. 2.3 g).

Foraging niche breadth: specialist or generalist?

Throughout *Pohlylepis* woodlands, the use of foraging microhabitats by some bird species was maintained while some others vary locally and/or regionally as reflected by niche breadth values. Based on breadth variation (or lack thereof), *O. fraseri* and *L. xenothorax* are considered specialists because they present relatively narrower niches that did not vary significantly across populations (Fig. 2.4 a, c, Table 2.3). Most bird species in the study were generalists in the use of foraging microhabitats, as evidenced by the relatively broader niche breadth. From these, *M. leucophrys* and *L. pileata* (Fig. 2.4 c, f, Table 2.3) were consistently broad in microhabitat use (i.e., no statistically differences in niche breadth across populations and/or regions), while *C. baroni*, *C. albicapilla*, *L. yanacensis*, *X. parina*, and *O. rufipectoralis*, varied in niche breadth across populations or regions (i.e., there were statistical differences in niche breadth values) (Fig. 2.4 b, d, e, g, Table 2.3). In general, intrapopulation variation in microhabitat use is observed in specialists and generalists' species (as reflected by SD values) (Fig. 2.4 a-g, Table 2.3).

Foraging niche plasticity: restricted or plastic?

Bird species had different patterns of niche plasticity across populations, as represented by the position of the c value obtained in the ordination (see methods). For instance, *O. fraseri*, *L. pileata*, *L. yanacensis*, and *X. parina* did not show significant differences in position across *Pohlylepis* woodlands, suggesting restriction in the foraging niche (Fig. 2.5 a,

c-e), whereas populations of *C. baroni/albicapilla*, *L. xenothorax*, *M. leucophrys* and *O. rufipectoralis* differed significantly in position across populations, suggesting plasticity in the foraging niche (Fig. 2.5 b, c, f, g).

Based on niche breadth values and foraging plasticity, insectivorous bird species associated with *Polylepis* woodlands presented four strategies: a) Specialist-restricted, b) Specialist-plastic, c) Generalist-restricted, and d) Generalist-plastic (Table 2.4).

Variation in ecological factors

Food resources abundance.- Abundance of arthropods in *Polylepis* bark, moss, and *Polylepis* foliage differed significantly across woodlands (Table 2.5) while *Gynoxys* and *Tristerix* foliage were not significantly different in arthropod abundance across woodlands (Table 2.5). Regional differences in food resources were also found for *Polylepis* bark, moss, and *Gynoxys* foliage. Basically, C. Blanca had fewer arthropods in moss and *Gynoxys* foliage, while C. Vilcanota had fewer arthropods in *Polylepis* bark (Table 2.5).

Arthropods in the bark of *Polylepis* trees were more abundant when compared with other microhabitats, excluding the humidity-dependent moss (Servat *unpub.*). In addition, *Polylepis* bark had a distinctive set of arthropods composed by free-living and weaving spiders, Pseudoscorpionida, and Dermaptera, which likely use the layers of *Polylepis* bark as a refuge that protects them against desiccation, a major problem for species at high elevations (Irons et al. 1993, Lencioni 2004). The other microhabitats included in the study were pretty distinctive in terms of prey (Servat *unpub.*), however not all microhabitats were present at each forest. Based on the presence/absence of microhabitats across *Polylepis*

woodlands, I considered, *Pohlylepis* bark and foliage predictable microhabitats, while *Gynoxys*, moss, and *Tristerix* were unpredictable across forests.

Floristic composition.- *Pohlylepis* woodlands contained a total of 50 plant species in 31 genera and 24 families (Servat, Chapter I). Plant species richness differed significantly across *Pohlylepis* woodlands (Table 2.6), with more species found in Llanganuco (average 12 plant species/100 individuals), Morococha (average 8 species /100 individuals) (C. Blanca), and Yanacocha (average 12 species/100 individuals) (C. Vilcanota) than in other forest sites (Table 2.6). Total number of species and individuals also differed among regions, with C. Occidental (the richest region), contributing to these differences (Table 2.6).

Vegetation structure.- Horizontal structure variables (*i.e.*, TBA, SD, DBH2, and DBH3) differed significantly across woodlands with exception of the number of small size trees (DBH1 > 10-20 cm dbh), and tree density (TD) that remain similar in all forests (Table 2.7). Regional differences were also found in all variables, except for the number of smaller and larger categories of tree sizes (DBH 1 > 10-20 cm, DBH3 > 30 cm, respectively) (Table 2.7). Basically, woodland differed in the basal area that *Pohlylepis* trees occupy (*e.g.*, Aquilpo, Yanacocha, and Yauí had more tree basal area than Llanganuco, Maticuna, Japari and Pumahuanca woodlands, Table 2.7). Vertical structure variables (*i.e.*, HEIGHT, FHDEN1, FHDEN2, and FHDEN3) were significantly different across woodlands and regions (Table 2.8).

Local and regional factors and foraging of insectivorous birds

In five of the seven models tested using Permute! (*i.e.*, *L. pileata*/*L. xenothorax*, *C. baroni*/*C. albicapilla*, *O. rufipectoralis*, *X. parina* and *M. leucophrys*), site similarities in foraging

ecology of insectivorous birds of *Polylepis* woodlands were partially explained by site similarities in food resources, accounting for 10 to 30 % of the variance observed (Table 2.9). For *X. parina*, site similarities in food resources ($R^2 = 0.26$), floristic composition (Partial $R^2 = 0.26$), and region (Partial $R^2 = 0.20$) partially explained site similarities in foraging ecology (Table 2.9). In *L. pileata/L. xenothorax*, food resources (Partial $R^2 = 0.11$) and vertical vegetation structure (Partial $R^2 = 0.32$) partially explained site similarities in foraging. Similarity in horizontal vegetation structure was the only predictor of similarities in foraging ecology of *L. yanacensis* (Partial $R^2 = -0.49$), the negative value indicates that foraging similarities were larger at sites less similar in horizontal vegetation structure. In addition to food resources, site similarities in foraging of *M. leucophrys* were also explained by region (Partial $R^2 = -0.25$), a significantly negative value indicates that similarities in foraging ecology were larger within region than across the three regions (Table 2.9). None of the factors measured were suitable predictors of foraging ecology of *O. fraseri*.

DISCUSSION

The foraging niche of insectivorous bird species associated with the *Polylepis* community varied from specialist-restricted (e.g., *O. fraseri*); specialist-plastic (e.g., *L. xenothorax*), generalist-restricted (e.g., *X. parina*); or generalist-plastic (e.g., *L. pileata*, *L. yanacensis*, *M. leucophrys*, and *O. rufipectoralis*).

Despite local and regional differences in measured factors, the foraging ecology of *O. fraseri* remained similar across forests and regions. Of all the bird species studied here, *O. fraseri* is the only one whose distribution is entirely restricted to *Polylepis* woodlands.

Consequently, *O. fraseri* may have evolved specialized searching and pursuit maneuvers (e.g., probing) and morphologies (e.g., longer, narrower, and flattened vertically bill) to forage in the multilayered bark of *Pohlylepis* trees (e.g., Ralston and Wainwright 1997, Emlen and DeJong 1981, Ferry-Graham 1998, Ferry-Graham et al 2001, Ferry-Graham et al 2002); such specializations would have been likely reinforced because of the absence of gene flow from any individuals outside of this forest type that arisen during isolation at very high elevation (with only trees of the genus *Pohlylepis* present), and the strategy may have remained unchanged since the time of speciation (Garcia-Moreno and Fjelds  2000). A conservative-specialist strategy seems to be influenced by history of taxa or morphological constraints as predicted by the “historical/morphological factors hypothesis”.

With the exception of *O. fraseri*, pair-site similarities in foraging of bird species track pair-site similarities in food resource abundance, and in some species, foraging similarities between sites were also related to similarities in floristic composition and vegetation structure. For example, *X. parina* foraging ecology appears to respond to local and regional variation in food resources and floristic composition of *Pohlylepis* woodlands. Variation in plant species composition likely translates into “architecturally” different microhabitats inhabited by arthropods, the primary food resources for birds (Table 2.6). Local differences in plant architecture likely constrain the ways in which a bird can search and capture prey (Recher 1969, Robinson and Holmes 1984, see Mac Nally 1995 for review). For instance, *Pohlylepis* foliage is a predictable microhabitat, rich in larvae and Diptera, which is commonly used by several species of foliage-gleaners. When *X. parina* forages in *Pohlylepis* foliage, it searches for prey reaching and gleaning for insects in any direction (up, down, upside-down). However, when *X. parina* uses *Gynoxys* foliage (a less predictable microhabitat in

Polylepis woodlands characterized by abundant Homoptera attached to the undersides of leaves) individuals begin foraging in the lower part of the plant and move their way up to the top, reaching and gleaning the undersides of leaves. Thus, *X. parina* switches foraging maneuvers locally in response to plant species. Similarly, regional variation in foraging of *X. parina* may also reflect adaptation to regional differences in plant species composition. For instance, the distribution of *Tristerix* plants (another microhabitat used by *X. parina*), is restricted to C. Blanca and C. Occidental. When *Tristerix* is present, *X. parina* forages in this microhabitat in a similar fashion than when it forages in *Polylepis* foliage, *Tristerix* is a parasitic plant growing on branches of *Polylepis* trees. The *Tristerix* microhabitat is rich in Diptera, but it is not present in all woodlands, and it is not present in the C. Vilcanota region. When examined across all sites, *X. parina* is a generalist because of its ability to use several microhabitats, but it is consistently restricted locally in foraging ecology in function of the microhabitats present at each site.

In contrast to *X. parina*, *L. xenothorax* is a specialist on *Polylepis* bark and foliage, but shows considerable foraging plasticity within and across populations, thus revealing its ability to adapt to changes in food resource abundance. The morphologically similar *L. pileata* is a sister species to *L. xenothorax*; *L. xenothorax* is endemic to southern Peru in the C. Vilcanota, while *L. pileata* is found in the northern and central Andes of Peru (Fjeldså 1992, Sibley & Monroe 1990, Remsen 2003). Unlike, *L. xenothorax*, *L. pileata* has a broader niche breadth (generalist). Comparatively speaking, arthropod abundance in *Polylepis* foliage was lower in woodlands from C. Blanca and C. Vilcanota. When *L. pileata* occurs in *Polylepis* woodlands with limited food resources, it uses more microhabitats (broader niche breadth) as predicted from optimality theory (MacArthur and Pianka 1966). Thus, prey-rich

microhabitats of C. Occidental may favor specialization in *L. pileata*, thus leading to narrower niche breadths than in relatively prey-poor C. Blanca. While site similarities in food resources may explain some of the variation in the foraging strategies used by *Leptasthenura* species, other factors need to be taken into consideration. The third species, *L. yanacensis*, is the most widely distributed, and co-occurs with either *L. pileata* or *L. xenothorax* respectively. In this study, when *L. yanacensis* is found with the generalist *L. pileata* its niche breadth seems to be narrower than when it co-occurs with the specialist *L. xenothorax*. These results suggest the potential importance of species interactions, such as competition for rich microhabitats or food resources, in shaping local patterns of foraging. Increased niche breadth in the presence of *L. xenothorax* may be a mechanism to avoid competition with the specialist on *Polylepis* foliage and bark (e.g., Cody 1974; Ford et al. 1986; MacArthur 1958; Recher 1989; Recher and Davis 1998; Wheeler and Calver 1996; Wiens 1989). However, specialization in this context is difficult to interpret, because subordinate competitors through competition with dominant ones may appear to be specialists, yet such individuals may be restricted to only a small subset of the available microhabitats or food resources. Overall results of this study suggest that differences in foraging ecology of most bird species associated with *Polylepis* woodlands respond to site differences in local factors (i.e., vegetation structure and abundance of food resources in *Polylepis* foliage) and, thus, follow the predictions generated by the “local/regional factor hypothesis”.

Ecological and evolutionary implications of different foraging strategies

Large-scale studies of species foraging that include several populations contribute to the understanding of a species' potential for adaptation, which is crucial for species survival

(Orr and Smith 1998; Lenormand 2002). In the present study foraging ecology of most insectivorous species associated with *Polylepis* woodlands responded locally to fluctuations in food resources, floristic composition and other factors, suggesting that populations of the same species may be subject to different selective pressures with subsequent ecological and evolutionary implications (e.g., Holbrook and Schmitt 1992). In this study, shifts in foraging microhabitats and maneuvers were associated with niche expansion or contraction of birds, which potentially (if heritable) could result in disruptive selection, evolution of reproductive isolation (Gibbons 1979, Seger 1985, Kondrashov and Mina 1986, Dieckmann and Doebeli 1999), and adaptive radiation (Schliwen et al. 1994; Schluter 2000, Losos 1994). Some previous work suggests that foraging specialization may be correlated with the rarity of a species or its vulnerability to extinction (Sierro & Arlettaz 1997, Vaughan 1997). This idea assumes that specialized species can rarely switch foraging ecology and that specialists face an elevated extinction risk because of their inability to change when faced with environmental variation, as have been shown for some taxa (phytophagous insects; *Ailuropoda melanoleuca*, Carter et al. 1999; Hopkins et al. 2002; *Mustela nigripes*, Powell et al. 1985; Dobson & Lyles 2000). If such is the case, then it may be possible to predict population responses to rapid changes in the environment based on the foraging strategy used. If foraging ecology of birds in the *Polylepis* system is correlated with the risk of extinction, then in the presence of stochastic events or fast changes in the environment, restricted-specialists such as *O. fraseri* might be prone to local extinction, due to its inability to adjust to local changes and therefore will be selected against (Stearns 1994). Meanwhile, plastic-generalist species might be seen as proxy to local adaptation because species may be able to track variation in local conditions (i.e., fluctuations in food resources, floristic

composition, or vegetation structure). At present, there is little evidence to confirm which strategy is more likely to adapt to environmental change, and most studies have failed to link generalist species with success in changing environments (e.g., Newsome and Noble 1986, Veltman *et al.* 1996). Moreover, the specialist-restricted strategy could be seen as greater efficiency in resource use and, thus, increased fitness (e.g., Sherry 1990). Under this view, plastic-generalist species are less efficient to adapt to novel or changing environments and then its risk of extinction will be higher (Mayr 1965, Myers 1986, Ehrlich 1989, Williamson 1996, Sol *et al.* 2002).

Intraspecific and interspecific studies of foraging, as some other trait, are important to determine how species respond to the combination of historical, regional (*i.e.*, biogeography), and present local environmental conditions (abiotic and biotic) in which species are embedded (e.g., Korona 1996, Travisano and Rainey 2000, Losos *et al.* 2003). Studies that treat conspecifics as ecological equivalents and use population average responses to make predictions regarding ecological and evolutionary consequences for species and communities ignore the variety of species' adaptations to cope with their biological demands (Bolnick 2003). Future studies regarding species' potential for adaptation to changing conditions also need to quantify the ecological and fitness consequences for the species, which is crucial for maintenance of systems modified at accelerated rates from human activities such as in the *Polylepis* system.

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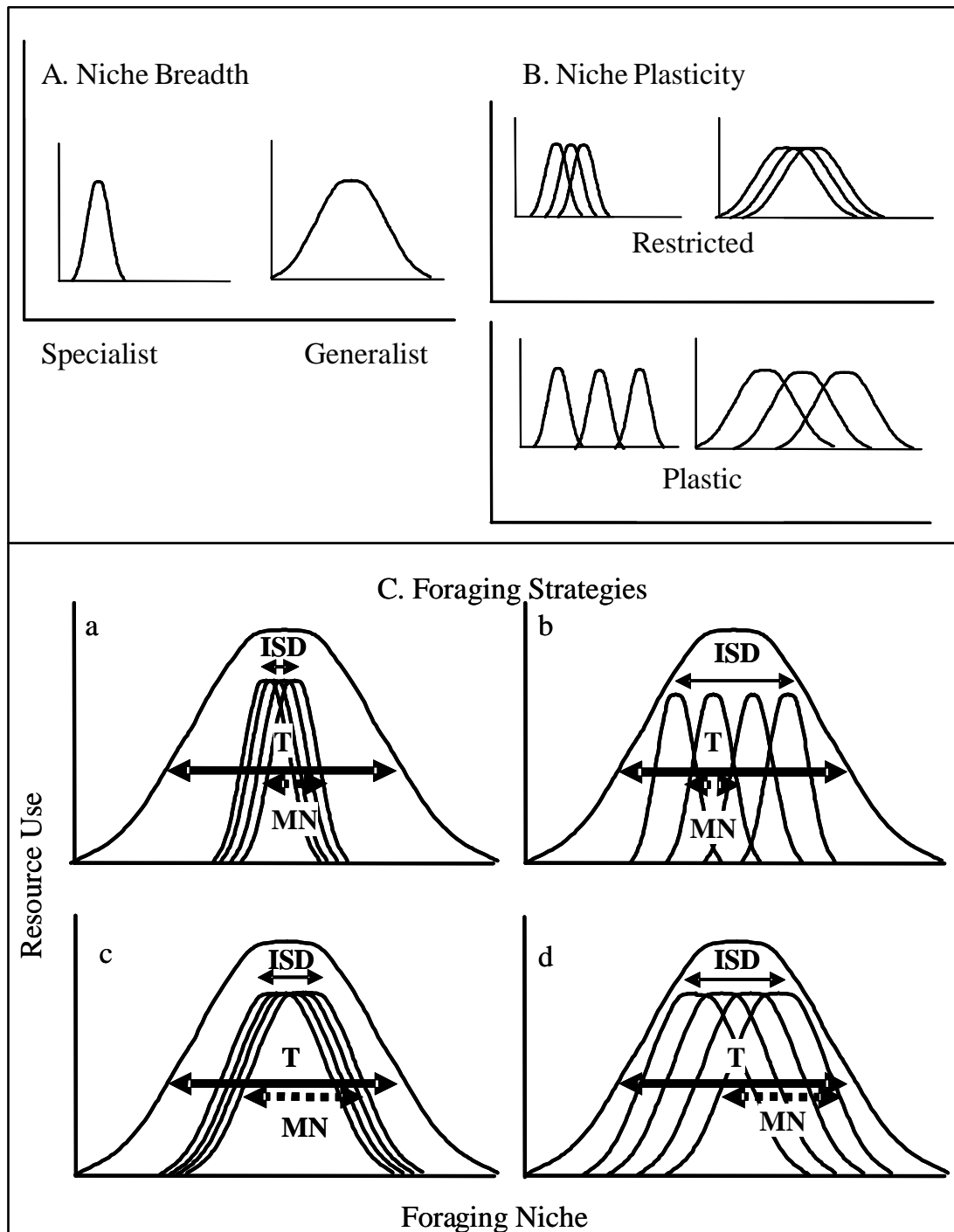
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Figure 2.1. Schematic diagrams of population niche breadth (A) and plasticity (B). Foraging strategies (C): a) Restricted-specialist, b) Plastic-specialist, c) Restricted-generalist, d) Plastic-generalist. ISD = Individuals SD, T = Total Niche breadth, MN = Mean Niche breadth.



(Modified from Bolnick *et.al* 2003)

Figure 2.2. Map of the Peruvian Andes showing study regions, *Polylepis* woodlands, and climate stations mentioned in text (in parenthesis are latitude, longitude, elevation (m), temperature ($^{\circ}$ C), precipitation (mm), and humidity (%)). (A).- C. Blanca: 1 = Ishinca, 2 = Aquilpo, 3 = Llanganuco, 4 = Morococha (B).- C. Occidental: 1 = Yauí, 2 = Maticuna, 3 = Japani, 4 = Quichas (C).- C. Vilcanota: 1 = Yanacocha, 2 = Sacsamonte, 3 = Pumahuanca, 4 = Quenuamonte. Contour line represents elevations above 3000 m. Stars are climate stations: (a) = Chinancocha ($9^{\circ}6'S$, $77^{\circ}40'W$, 3850 m, $8^{\circ}C$, 642 mm, 64%), (b) = Lampas Alto ($10^{\circ}0'S$, $77^{\circ}20'W$; 4030 m, $6^{\circ}C$, 737 mm, 67%), (c) = Oyón ($10^{\circ}33'S$, $76^{\circ}45'W$, 3631 m, $9^{\circ}C$, 538 mm), (d) = Urubamba ($13^{\circ}18'S$, $72^{\circ}7'W$, 2870 m, $14^{\circ}C$, 494 mm, 66 %), (e) = Calca ($13^{\circ}20'S$, $71^{\circ}57'W$, 2859 m, $15^{\circ}C$, 437 mm).

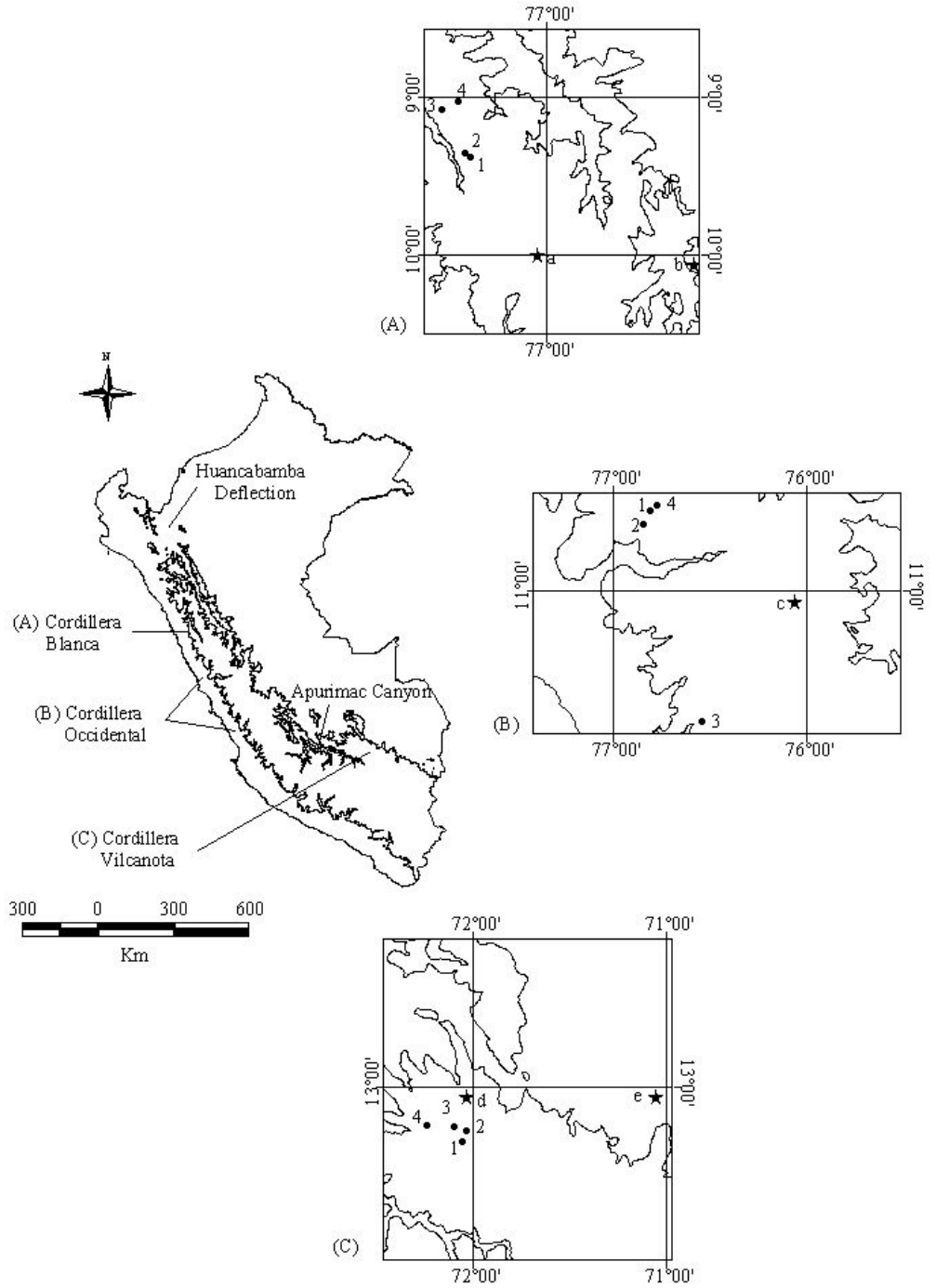


Figure 2.3. Proportional use of foraging categories by arboreal-insectivore birds associated with *Pohlylepis* woodlands. In legend are the names of the 25 categories, the first two letters indicate the microhabitat (PB = *Pohlylepis* bark, PF = *Pohlylepis* foliage, GF = *Gynoxys* foliage, GB = *Gynoxys* bark, DB = Dead branch, TF = *Tristerix* foliage, MS = moss, SH = shrubs, and GR = ground) and the last two letters indicate the maneuvers (GL= glean, PR = probe, RE = reach, HG = hover-glean, SG = sally-glean, and PG = pull-glean), with the only exception of AEHWC = aerial hawking in canopy, and AEHWU = aerial hawking in the understory. Site codes are from North to South: AQ = Aquilpo, IS = Ishinca, MO = Morococha, LL = Llanganuco (in C. Blanca), UI = Yauí, MA = Maticuna, JA = Japani, KI = Quichas (in C. Occidental), YA = Yanacocha, SA = Sacsamonte, PU = Pumahuanca, QE = Quenuamonte (in C. Vilcanota). Numbers above bars indicate the number of foraging categories used by the population at a particular forest.

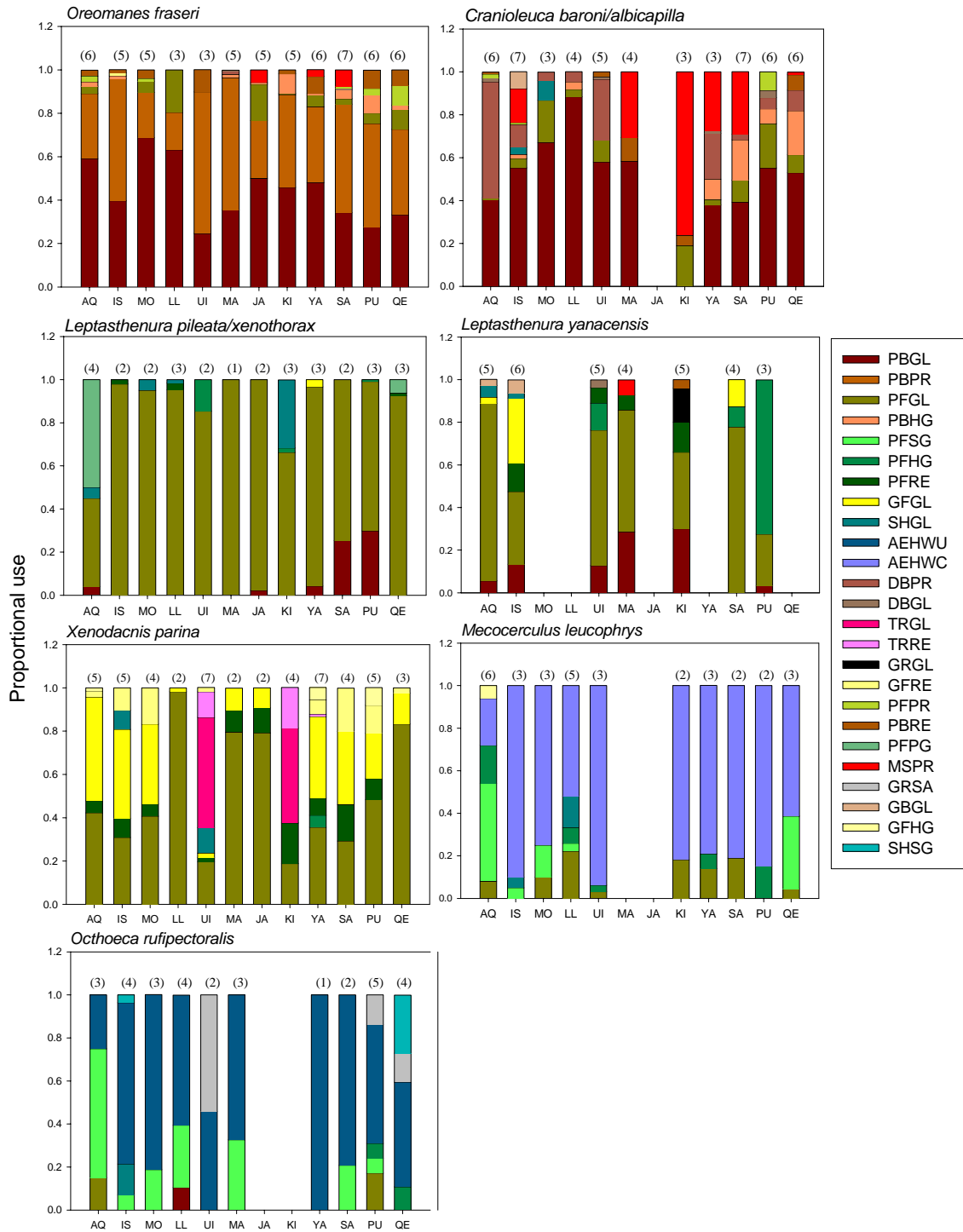


Figure 2.4. Levin's mean niche breadth (\pm SD) for each population of insectivorous bird species associated with *Polylepis* woodlands. Low or high values of niche breadth denote specialist or generalist species, respectively. (*) The asterisk represents populations of *L. xenothorax*

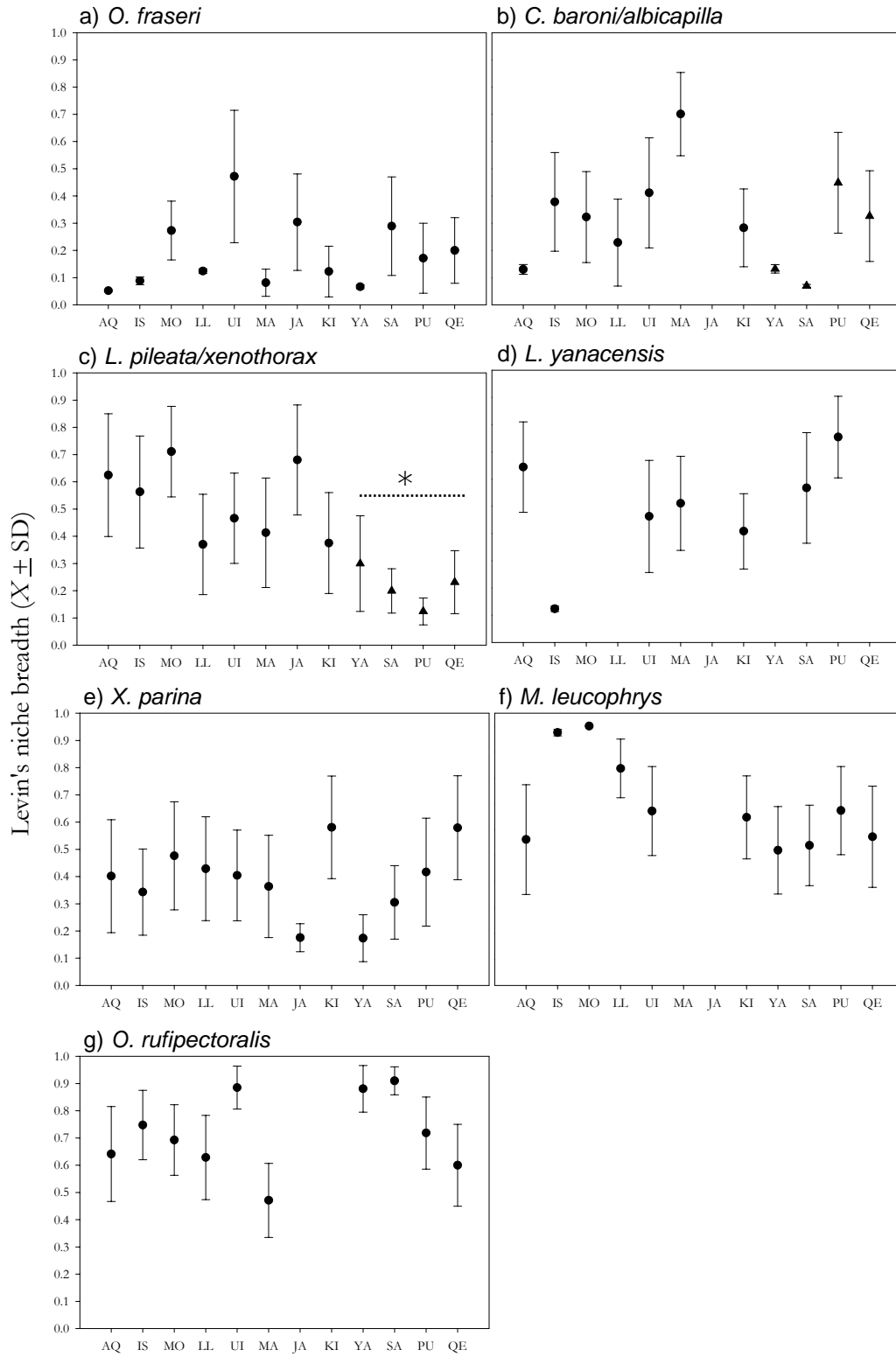


Figure 2.5. Foraging niche plasticity of insectivorous bird species. Plasticity is represented by the mean ϵ value (\pm SD) (see text for calculations). Significance of hierarchical MANOVA (F) results for regional and local patterns of plasticity for every bird species is shown.

Asterisks indicate significance levels: (*) = $P < 0.01$, (**) $P < 0.001$, NS = no significance.

AQ = Aquilpo, IS = Ishinca, MO = Morococho, LL = Llanganuco, UI = Yauí, MA =

Maticuna, JA = Japani, KI = Quichas, YA = Yanacocho, SA = Sacsamonte, PU =

Pumahuanca, QE = Quenuamonte.

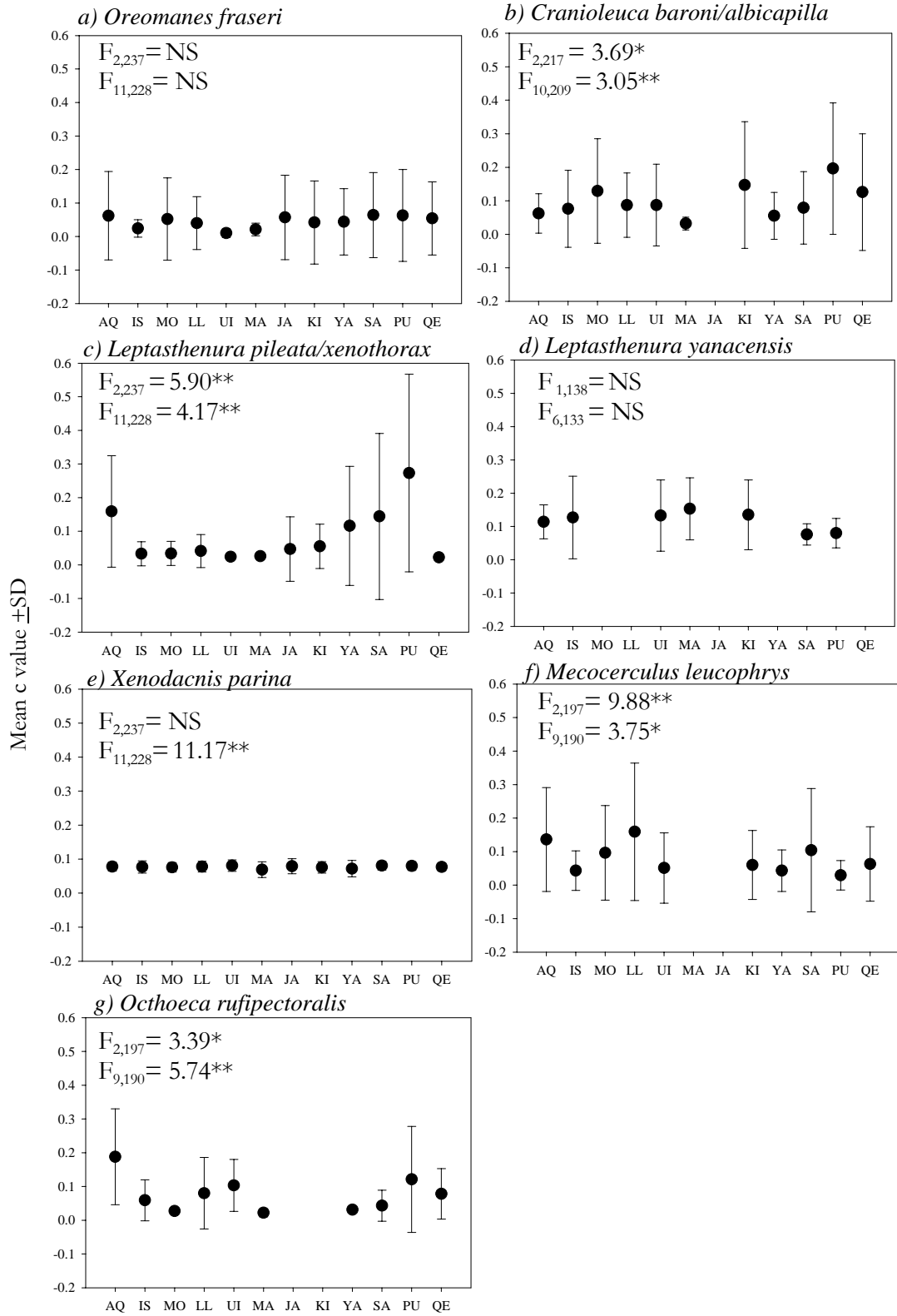


Table 2.1. *Polylepis* woodlands in the Andes of Peru selected for the present study and dates of data collection during the two years of study. Approximate woodland size is based on aerial photographs.

Woodlands	~Size (ha)	Latitude (S)	Longitude (W)	Elevation (m)	1997	1998
Aquilpo	250	09°21'	77°30'	4075	Aug 3-12	Jun 9-15
Ishinca	150	09°22'	77°28'	3800	Oct 16-23	Jun 15-21
Morococha	150	09°01'	77°32'	3836	Aug 17-27	Sep 22-26
Llanganuco	150	09°05'	77°38'	3850	Oct 27-Nov 5	Sep 28-30
Yauí	200	10°35'	76°48'	4184	May 16-21	Sep 13-18
Maticuna	200	10°39'	76°50'	3990	Nov 18-23	Sep 8-13
Japani	300	11°41'	76°31'	4140	Nov 28-Dec 2	Jun 25-Jul 1
Quichas	50	10°33'	76°46'	4200	----	Jul 4-9
Yanacocha	120	13°17'	72°03'	4012	Jul 1-11	Aug 16-22
Sacsamonte	50	13°13'	72°02'	3926	Jul 14-23	May 27-Jun 2
Pumahuanca	50	13°12'	72°05'	4110	Sep 6-15	Jul 17-23
Quenuamonte	50	13°11'	72°13'	3812	Sep. 18-26	Aug 27-Sep 2

Table 2.2. Insectivorous species associated with *Polylepis* woodlands. The asterisk after the species name indicates the bird species and subspecies included in the study. *Polylepis* woodlands: AQ=Aquilpo, IS=Ishinca, MO=Morococho, LL=Llanganuco, UI=Yauai, MA=Maticuna, JA=Japani, KI=Quichas, YA=Yanacocho, SA=Sacsamonte, PU=Pumahuanca and QE=Quenuamonte. (1) Taxonomy follows Stotz et al. (1996); (2) Abundance: C = common, species that throughout their range of distribution occur in moderate to large numbers (densities of more than 5-6 individuals/ha) and are found easily during brief periods of time (1-2 days). U = Uncommon, less numerous (densities of 2-4 individuals/ha) detected in proper habitat. R=rare, species scarce and seldom encounter even during prolonged stays in the field. Many of these species are territorial or patchily distributed and occur in small number (densities of 1-2/ha) throughout their range of distribution; (3) Habitat: BU=bushes, FE=*Polylepis* forest edge, FI = *Polylepis* forest interior; (4) Strata: U = understory, SC = sub-canopy, C = canopy, A = aerial.

Family (1)	Species	Abundance (2)												Habitat (3)	Strata (4)			
		Aq	Is	Mo	Ll	Ui	Ma	Ja	Ki	Ya	Sa	Pu	Qe					
Furnariidae	<i>Leptasthenura yanacensis</i> *	U	C			C	C		C			U	U	BU, FE, FI	U, SC, C			
	<i>L. xenothorax</i> *											C	C	C	C	BU, FI	U, SC	
	<i>L. pileata cajabambae</i> *	U	U	C	U												BU, FE, FI	U, SC
	<i>L. pileata pileata</i> *					U	C	C	U								BU, FE, FI	U, SC
	<i>Cranioleuca albicapilla</i> *											C	C	C	C		FI	U, SC, C
	<i>C. baroni zaratensis</i> *					U	C		C								FI	U, SC, C
	<i>C. baroni baroni</i> *	C	C	C	C												FI	U, SC, C
Tyrannidae	<i>Mecocerculus leucophrys pallidior</i> *	C	C	U	U												FI	SC, C, A
	<i>M. leucophrys spp.</i> *					C	R		U								FI	SC, C, A
	<i>M. l. brunneomarginatus</i> *									U	R	U	R				FI	SC, C, A
	<i>Anairetes alpinus</i>	U	U			R				U	R	U	R				FI	SC, C, A
	<i>A. parulus</i>									U			U				BU, FI	SC, C, A
	<i>A. nigrocristatus</i>			U													FE, FI	U, SC, C, A
	<i>Octoeca rufipectoralis centralis</i> *	C	U	C	C												FE, FI	SC, C
	<i>O. rufipectoralis.spp.</i> *					U	R										FE, FI	SC, C
	<i>O. r. tectricialis</i> *									C	U	C	C				FE, FI	SC, C
	<i>O. oenantoides</i>	U	U	U		C	R	C	U	U	U						FE, FI	SC, C
Thraupinae	<i>Oreomanes fraseri</i> *	U	C	U	C	U	U	C	C	C	C	C	C				FI	U, SC
	<i>Xenodacnis parina petersi</i> *	C	C	C	C	U	U	R	U								FE, FI	U, SC
	<i>X. p. parina</i> *									C	C	C	C				FE, FI	U, SC
Emberizinae	<i>Poospiza alticola</i>	C	U	C	C												FE, FI	U, SC, C
Total species number		10	10	9	7	9	8	4	7	9	9	8	8					

Table 2.3. Inter and intraspecific variation in niche breadth of arboreal-insectivore birds across forests nested within three regions. The niche breadth value of each individual bird for each population was used as replicates in Hierarchical *MANOVA* tests (F). Asterisks (*) indicate significance levels: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$ after Tukey Post hoc test.

Forest	<i>O.fraseri</i>	<i>C.baroni/C. albicapilla</i>	<i>L.pileata/L. xenothorax</i>	<i>L.yanacensis</i>	<i>X.parina</i>	<i>O.rufipectoralis</i>	<i>M.leucophrys</i>
Aquilpo	0.13±0.133	0.05±0.061b	0.62±0.475	0.64±0.408b	0.40±0.456	0.56±0.460	0.64±0.417
Ishinca	0.09±0.120	0.38±0.426	0.56±0.454	0.12±0.100a	0.34±0.398	0.98±0.112 ^a	0.75±0.357
Morococha	0.27±0.329	0.32±0.409	0.71±0.408	NP	0.48±0.445	0.99±0.010 ^b	0.69±0.360
LLanganuco	0.12±0.092	0.23±0.400	0.37±0.429	NP	0.43±0.437	0.84±0.336	0.63±0.393
C. Blanca	0.15±0.202	0.25±0.372	0.57±0.452	0.38±0.394	0.41±0.429	0.84±0.334	0.68±0.379
Yauí	0.47±0.493a	0.41±0.449a	0.47±0.407	0.46±0.454ab	0.40±0.408	0.67±0.414	0.89±0.281
Maticuna	0.08±0.223b	0.70±0.391	0.41±0.448	0.51±0.416b	0.36±0.433	NP	0.47±0.369
Japani	0.30±0.421	NP	0.68±0.449	NP	0.18±0.227	NP	NP
Quichas	0.12±0.305	0.28±0.378	0.38±0.430	0.41±0.372ab	0.58±0.434	0.65±0.400	NP
C. Occidental	0.24±0.400	0.47±0.438**	0.48±0.442	0.46±0.410	0.38±0.405	0.66±0.402	0.68±0.386
Yanacocha	0.07±0.084b	0.13±0.124	0.30±0.419	NP	0.17±0.293	0.52±0.411	0.88±0.293
Sacsamonte	0.29±0.425	0.07±0.072	0.20±0.286	0.57±0.451b	0.30±0.367	0.54±0.394	0.91±0.227
Pumahuanca	0.17±0.359	0.45±0.430 ^b	0.12±0.223	0.75±0.387b	0.42±0.445	0.67±0.412	0.72±0.364
Quenuamonte	0.20±0.347	0.33±0.408	0.23±0.340	NP	0.58±0.437	0.57±0.442	0.60±0.388
C. Vilcanota	0.18±0.334	0.24±0.336	0.21±0.325***	0.66±0.425***	0.37±0.411	0.58±0.411	0.78±0.342*
MANOVA F _{region}	NS	7.03**	6.90**	5.39***	NS	10.75***	3.48*
MANOVA F _{local}	NS	4.62***	NS/NS	***	2.46**	3.37**	NS

Table 2.4. Foraging strategies of insectivorous birds. Data in the table includes foraging niche breadth (Levin's index) and plasticity results for each bird species based on the statistical significance of hierarchical *MANOVA* tests (see text for calculations). (n) = number of populations. Asterisks indicate significance levels: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$ after Tukey Post hoc test..

Bird Species	Niche breadth in microhabitat use		Niche plasticity in c value position	Foraging strategy
	Niche range size	MANOVA $F_{(local)}$	MANOVA $F_{(local)}$	
<i>Oreomanes fraseri</i> (n=12)	0.05-0.47	NS	NS	Specialist-restricted
<i>Craniolenca baroni</i> / <i>C. albicapilla</i> (n=12)	0.13-0.70	4.62**	3.05***	Generalist-plastic
<i>Leptasthenura pileata</i> (n=8)	0.37-0.71	*	NS	Generalist-restricted
<i>L. xenothorax</i> (n=4)	0.12-0.30	NS	4.17***	Specialist-plastic
<i>L. yanacensis</i> (n=7)	0.12-0.75	5.39**	NS	Generalist-restricted
<i>Xenodacnis parina</i> (n=12)	0.17-0.58	2.46*	NS	Generalist-restricted
<i>Mecocerculus leucophrys</i> (n=10)	0.47-0.91	NS	3.75**	Generalist-plastic
<i>Octoeca rufipectoralis</i> (n=10)	0.52-0.99	3.37	5.74***	Generalist-plastic

Table 2.5. Food resources abundance (arthropods/microhabitat). Hierarchical MANOVA results for arthropod abundance at each microhabitat across 12 woodlands and 3 regions of study based on two replicate plots per forest. Significance of F-values for local and regional effects is indicated as: ** = $P < 0.01$, *** = $P < 0.001$, NS = No significant differences. Superscripts following means indicate differences across sites (a, b, c) or regions (A, B) after post-hoc Tukey test. NP = not present.

Forests and Regions	Arthropod abundance per microhabitat				
	<i>Polylepis</i> foliage	<i>Polylepis</i> bark	Moss	<i>Gynoxys</i> foliage	<i>Tristerix</i> foliage
Aquilpo	41.0±11.3 ^a	77.5±21.9 ^a	139.0±11.3	25.0±0.0	5.5±4.9
Ishinca	58.5±0.7	76.0±22.6 ^a	141.5±13.4	72.5±62.9	20.0±25.5
Morococha	69.0±32.5	134.0±8.5	65.5±4.9 ^a	44.0±15.5	62.5±30.4
Llanganuco	57.0±26.8	89.0±11.3	50.0±12.7 ^a	36.0±21.2	NP
C. Blanca	56.4±19.7 ^B	119.0±59.2 ^B	99.0±45.3 ^A	44.4±31.9 ^A	29.3±31.9
Yauli	70.5±10.6	144.5±40.3	84.0±8.5	11.0±0.0	68.0±65.1
Maticuna	120.5±2.1	231.5±44.5 ^b	436.0±120.2 ^b	75.0±72.1	30.0±16.9
Japani	244.5±7.8 ^c	214.5±74.2	205.5±45.9	NP	47.0±63.6
Quichas	142.5±34.6 ^b	109.5±0.70	83.5±34.6	158.5±37.1	47.5±31.8
C. Occidental	144.5±69.2 ^A	175.0±64.4 ^A	202.3±161.8 ^B	81.5±75.4 ^B	48.1±39.7
Yanacocha	61.5±3.5	108.0±41.0	256.5±60.1	88.5±41.7	NP
Sacsamonte	58.0±22.6	53.5±13.4	179.5±48.8	81.5±12.0	NP
Pumahuanca	129.0±12.7	71.5±9.2 ^a	153±11.3	120±9.2	NP
Quenuamonte	53.0±9.9	119.5±28.9 ^a	138.5±57.3	57±39.6	NP
C. Vilcanota	75.4±34.8 ^B	88.1±34.8 ^B	181.9±60.9 ^B	86.9±33.1 ^B	NP
MANOVA Local F _{11,24}	20.1***	5.6**	9.6***	NS	NS
MANOVA Region F _{2,10}	***	19.4***	16.2***	8.1**	--

Table 2.6. Floristic composition across *Polytepis* woodlands. Hierarchical MANOVA results for plant species richness and abundance across regions and forests. Asterisks indicate levels of significance: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, NS = no significance. Superscripts following means indicate differences across sites (a, b, c) or regions (A, B) after Post hoc Tukey's test.

Forests and Regions	Floristic Variables	
	Species number	Individuals number
Aquilpo	4.5±0.70 ^{ab}	260.0±25.45 ^{ab}
Ishinca	5.0±1.41 ^{ab}	318.0±15.55 ^{abc}
Morococha	8.5±2.12 ^{abc}	338.5±30.40 ^{abc}
Llanganuco	14.5±0.70 ^c	325.0±15.55 ^{abc}
C. Blanca	8.12±4.38 ^B	310.3±36.36 ^{AB}
Yauí	3.5±3.53 ^a	187.5±19.09 ^{ab}
Maticuna	5.5±0.70 ^{ab}	379.5±102.53 ^{bc}
Japaní	3.0±0.00 ^a	133.0±7.07 ^a
Quichas	3.5±0.70 ^a	253.5±108.18 ^{ab}
C. Occidental	3.8±1.72 ^A	238.3±113.58 ^A
Yanacocha	12.5±4.94 ^b	518.0±137.17 ^c
Sacsamonte	7.0±2.82 ^{ab}	214.0±31.11 ^{ab}
Pumahuanca	5.0±0.00 ^{abc}	307.5±2.12 ^{abc}
Quenuamonte	5.5±0.70 ^{abc}	332.0±5.65 ^{abc}
C. Vilcanota	7.5±3.85 ^B	342.8±129.34 ^B
<i>MANOVA</i> Local $F_{9,12}$	5.16**	5.08**
<i>MANOVA</i> Region $F_{2,12}$	6.17**	9.36**

Table 2.7. Multivariate hierarchical ANOVA results for horizontal vegetation structure variables. Means and SD are shown for all variables across 12 woodlands based on two replicate plots. Significance of F-values for local and regional effects is indicated as * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. Superscripts following means indicate differences across sites (a, b, c, d, e) or regions (A, B) according to Tukey multiple comparison among means test. TBA = total basal area (800 m^2), TD = tree density (# trees / 800 m^2), SD = shrub density (# shrubs / 800 m^2), DBH 1 = number of individuals in size class 1 (> 10 – 20 cm dbh), DBH 2 = number of individuals in size class 2 (> 20 - 30 cm dbh), DBH 3 = number of individuals in size class 3 (> 30 cm dbh). AC = absent category. NS = No significant differences.

Forests and Regions	Horizontal Vegetation Structure Variables					
	TBA	TD	SD	DBH1	DBH2	DBH 3
Aquilpo	537.5 ± 53.84 ^b	104.5 ± 12.02	165.0 ± 0.00 ^{ab}	40.5 ± 4.90	15.5 ± 2.12 ^{ab}	0.5 ± 0.70 ^b
Ishinca	340.3 ± 61.85 ^{ab}	91.0 ± 19.79	269.0 ± 11.51 ^{ab}	56.6 ± 12.02	31.5 ± 7.77 ^{abc}	3.0 ± 0.00 ^b
Morocochoa	175.5 ± 76.57 ^a	70.5 ± 34.64	268.5 ± 45.96 ^{ab}	54.0 ± 31.11	16.0 ± 2.82 ^{ab}	0.5 ± 0.70 ^b
Llanganuco	157.4 ± 18.51 ^a	56.5 ± 6.36	264.5 ± 2.12 ^{ab}	56.6 ± 13.43	39.5 ± 2.12 ^{bc}	8.5 ± 3.53 ^a
C. Blanca	302.7 ± 169.31 ^A	80.6 ± 25.35 ^{AB}	241.7 ± 50.67 ^{AB}	51.8 ± 5.44	25.6 ± 11.57 ^A	3.1 ± 3.75
Yauí	363.7 ± 12.19 ^{ab}	83.0 ± 2.82	101.0 ± 72.12 ^a	45.5 ± 7.77	33.5 ± 6.36 ^{abc}	4.30 ± 1.51 ^b
Maticuna	59.4 ± 42.09 ^a	42.0 ± 24.04	273.0 ± 47.07 ^{ab}	40.5 ± 23.33	1.5 ± 0.70 ^a	AC
Japani	75.3 ± 10.75 ^a	48.5 ± 3.53	32.5 ± 13.43 ^a	46.0 ± 2.82	2.5 ± 0.70 ^a	AC
Quichas	131.0 ± 19.68 ^a	65.5 ± 6.36	175.5 ± 132.22 ^{ab}	57.0 ± 11.51	8.0 ± 4.24 ^{ab}	0.5 ± 0.70 ^b
C. Occidental	157.3 ± 131.82 ^B	59.7 ± 19.52 ^A	145.5 ± 124.38 ^A	47.2 ± 12.13	11.5 ± 14.21 ^B	1.1 ± 1.88
Yanacocha	550.4 ± 213.66 ^b	149.0 ± 35.35	463.0 ± 79.60 ^b	82.5 ± 9.19	65.0 ± 25.45 ^c	1.5 ± 0.70 ^b
Sacsamonte	350.6 ± 106.08 ^{ab}	56.0 ± 9.89	160.5 ± 41.71 ^{ab}	25.0 ± 9.89	24.0 ± 4.24 ^{ab}	7.0 ± 4.24 ^b
Pumahuanca	175.7 ± 15.43 ^a	85.5 ± 14.84	189.0 ± 80.61 ^{ab}	72.5 ± 20.50	12.0 ± 4.24 ^{ab}	AC
Quenuamonte	370.0 ± 162.58 ^{ab}	101.5 ± 51.61	251.5 ± 27.57 ^{ab}	67.5 ± 44.54	26.5 ± 9.19 ^{ab}	4.0 ± 4.24 ^b
C. Vilcanota	361.7 ± 177.37 ^A	98.0 ± 43.58 ^B	266.0 ± 148.04 ^B	61.8 ± 30.34	31.8 ± 23.70 ^A	3.1 ± 3.64
<i>ANOVA</i> Local $F_{9,12}$	6.03**	NS	2.90*	NS	7.90***	4.16*
<i>ANOVA</i> Region $F_{2,12}$	10.73**	5.29*	4.43*	NS	11.70**	NS
MANOVA Local $F_{9,12} = 3.33^*$						
MANOVA Region $F_{2,12} = NS$						

Table 2.8. Hierarchical MANOVA results for vertical vegetation structure variables. Means and SD are shown for all variables across 12 woodlands based on two replicate plots.

Significance of F-values for local and regional effects is indicated as: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, NS = No significant differences. Superscripts following means indicate differences across sites (a, b, c, d, e) or regions (A, B) according to Post-hoc Tukey's test. FHDEN1 = foliage height density or proportional coverage at $> 0 - 2$ m, FHDEN2 = foliage height density at $> 2 - 6$ m, FHDEN3 = foliage height density at $> 6 - 10$ m, HEIGHT = mean tree height (m). ND = No data available.

Forests and Regions	Vertical Vegetation Structure Variables			
	FHDEN1	FHDEN2	FHDEN3	HEIGHT
Aquilpo	0.10 \pm 0.07 ^a	0.17 \pm 0.02 ^a	0.72 \pm 0.05 ^{de}	12.9 \pm 2.55 ^b
Ishinca	0.09 \pm 0.02 ^a	0.10 \pm 0.09 ^a	0.80 \pm 0.07 ^e	7.6 \pm 0.11 ^{ab}
Morococha	0.33 \pm 0.08 ^{ab}	0.42 \pm 0.02 ^{abc}	0.24 \pm 0.06 ^{abc}	8.4 \pm 1.59 ^{ab}
Llanganuco	0.34 \pm 0.01 ^{ab}	0.47 \pm 0.09 ^{abc}	0.18 \pm 0.08 ^{ab}	4.4 \pm 1.56 ^a
C. Blanca	0.21 \pm 0.13	0.29 \pm 0.17 ^A	0.48 \pm 0.30 ^A	8.3 \pm 3.48
Yauí	0.10 \pm 0.06 ^a	0.29 \pm 0.01 ^{ab}	0.60 \pm 0.04 ^{cde}	7.6 \pm 0.36 ^{ab}
Maticuna	0.56 \pm 0.16 ^b	0.42 \pm 0.14 ^{abc}	0.01 \pm 0.02 ^a	4.5 \pm 2.88 ^a
Japani	0.23 \pm 0.04 ^a	0.71 \pm 0.02 ^c	0.05 \pm 0.06 ^a	7.3 \pm 3.69 ^{ab}
Quichas	0.26 \pm 0.07 ^{ab}	0.59 \pm 0.00 ^{bc}	0.14 \pm 0.07 ^{ab}	6.8 \pm 0.94 ^{ab}
C. Occidental	0.28 \pm 0.19	0.50 \pm 0.18 ^B	0.20 \pm 0.25 ^B	6.6 \pm 2.22
Yanacocha	0.17 \pm 0.08 ^a	0.26 \pm 0.12 ^{ab}	0.56 \pm 0.20 ^{cde}	7.9 \pm 1.24 ^{ab}
Sacsamonte	0.16 \pm 0.08	0.34 \pm 0.22	0.50 \pm 0.14 ^{bcd}	8.8 \pm 1.75 ^{ab}
Pumahuanca	0.30 \pm 0.04 ^{ab}	0.45 \pm 0.11 ^{abc}	0.25 \pm 0.07 ^{abc}	7.0 \pm 0.48 ^{ab}
Quenuamonte	0.28 \pm 0.09 ^{ab}	0.37 \pm 0.01 ^{abc}	0.35 \pm 0.08 ^{abcd}	7.4 \pm 0.53 ^{ab}
C. Vilcanota	0.22 \pm 0.09	0.35 \pm 0.12 ^A	0.41 \pm 0.16 ^A	7.8 \pm 1.12
<i>ANOVA</i> Local F _{9,12}	6.18**	4.84**	14.64***	3.00*
<i>ANOVA</i> Region F _{2,12}	NS	9.36***	19.23***	NS
MANOVA Local F _{9,12} = 2.46**				
MANOVA Region F _{2,12} = NS				

Table 2.9. Mantel tests using 999 permutations and the program Permute (Casgrain 1998).

Each line in the table is a model that examines the influence of region, floristic compositions, vegetation structure, and arthropod abundance, on bird species foraging. n= number of pair site combinations used in the model (see text for calculations). Partial regression coefficients for each predictor variable and overall model R^2 are provided.

Significance of models is indicated by: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, NS = No significant differences.

<i>Models</i>	Predictor Variables					Overall R ²
	Region	Floristic composition	Horizontal structure	Vertical structure	Arthropod abundance	
<i>Oreomanes fraseri</i> (n=66)	0.034	0.087	-0.108	0.060	0.162	NS
<i>Cranioleuca baroni/albicapilla</i> (n=44/22)	0.160	-0.022	0.087	0.067	0.385***	0.15**
<i>Leptasthenura pileata xenothorax</i> (n=44/22)	-0.047	-0.030	-0.186	0.316**	0.114**	0.10**
<i>Leptasthenura yanacensis</i> (n=21)	0.114	0.112	-0.494*	-0.280	-0.089	0.24*
<i>Xenodacnis parina</i> (n=55)	0.203*	0.259**	-0.119	0.020	0.258**	0.15**
<i>Mecocerculus leucophrys</i> (n=45)	-0.246*	-0.005	-0.186	-0.066	0.468**	0.30**
<i>Octoeca rufipectoralis</i> (n=45)	-0.050	-0.196	-0.110	0.179	0.406**	0.16**

CHAPTER THREE

BIRD ASSEMBLAGE STRUCTURE IN THE *POLYLEPIS* COMMUNITY

Much of the past four decades of community ecology have been devoted to the analyses of community structure and organization (Diamond 1975, Connor and Simberloff 1979, Tilman 1982, 1988, Wiens 1986, 1989, Ricklefs 1987, Drake 1990, Cornell and Lawton 1992, Ricklefs and Schluter 1993, Losos 1994, 1998, Brown 1995, Huston 1999, Hubbell 2001, Leibold and Chase 2003). Yet, questions regarding whether communities are assembled randomly or by repeatable processes, how local conditions and regional contingency influence community organization, and the extent to which patterns of functional organization are repeated in space and time, have remained poorly resolved issues (Ricklefs and Schluter 1993, Brown 1995, Huston 1999, Hubbell 2001, Leibold and Chase 2003).

Our perceptions of community organization are influenced by a historical dichotomy of “individualistic” versus “organismal” classifications. Clements (1916) compared the plant community to an organism, “able to essentially reproduce its component parts”, whereas Gleason (1926) argued that a plant community is “scarcely even a vegetation unit, but merely a coincidence of the range of species”. Presently, the individualistic-organismal debate has been invigorated by the “neutral” and “niche” based models of community ecology. Neutral models (Hubbell 2001) view all species as equal or functionally equivalent, so they exert similar effects both on populations and on community organization. In contrast, niche-based

models grant species particular properties, and thus, recognize species as functionally distinct, with unique or non-substitutable roles (Chave et al. 2002, Chase and Leibold 2003).

Regardless of the debate over its nature, the complexity of natural communities makes it unlikely they function only as either groups of individual species present because of individual tolerances, or as assemblages of perfectly integrated species (Ricklefs 1987, Ricklefs and Schluter 1993, Ricklefs 2001). Instead, communities are regarded as a template from which a large number of local (e.g., past and present ecological processes), and/or historical factors (i.e., those that shaped the community from its beginning such as dispersal, speciation, migration, and extinction), which operate at different spatial and temporal scales, convene to shape particular aspects of their structure and organization (Vuilleumier and Simberloff 1980, Wiens 1986, 1989, Ricklefs 1987, Ricklefs and Schluter 1993, Losos 1994, 1998, Brown 1995, Huston 1999, Ricklefs 2001).

Analyses of community structure are conventionally made by breaking down groups of species (not necessarily related taxonomically) into “functional groups” or “guilds” (Root 1967), with the underlying assumption that the relationship between species and function is intimately linked (i.e., species with similar ecological attributes seem to act or respond to environmental variation in similar ways) (Walker 1992, Lawton and Brown 1994, see review in Chase and Leibold 2003). Although, guilds are considered to be “identifiable” and “constant” within a community, guilds are not static in space and time and, it is precisely their dynamic nature that makes them relevant to understand community structure (e.g., McNaughton 1978, Cornell y Kahn 1989, Mac Nally 1994) and organization (e.g., Jaksic and Delibes 1987, Jaksic and Medel 1990, Jaksic et al. 1993, Marti et al. 1993). A wide variety of criteria and levels of subdivision have been used to make assignments of species into guilds to describe community

structure (Karr 1971, 1976, 1980, Terborgh 1986, Szaro and Balda 1979, Blake 1983, Bradley and Bradley 1983, Manuwal 1983, Recher and Holmes 1985). However, given that energy acquisition is paramount to species survival and fitness, foraging ecology has been the prevalent way to group species into guilds (e.g., Root 1967, Morse 1971, Holmes et al. 1979, Sherry 1979, 1982, Holmes and Recher 1986, Landres and MacMahon 1983, Wiens 1983, Brown 1989, Mac Nally 1994).

Fluctuation in abiotic (e.g., temperature, wind, Cody 1985, Wiens 1989) and biotic factors, such as vegetation structure (e.g., vertical zonation of vegetation; MacArthur and MacArthur 1961, MacArthur et al. 1962, Robinson and Holmes 1984, McNally 1994, Huston 1994), floristic composition (e.g., the richness and relative number of floristic elements; Orians 1969, Recher 1969, James and Wamer 1982, Rotenberry 1985, Whitmore 1975, James et al. 1984, Tomoff 1974), available food resources (Morse 1977, Jaksic 1981, Wiens 1983, 1989, Bradley and Bradley 1985) and species interactions (e.g., Connell 1983, Schoener 1983) through its effects on foraging ecology of species, likely influence community structure (e.g., modifying species composition and/or abundance within guilds).

Studies that describe the extent of spatial variation in the structure of communities and the factors in which the community is embedded are insightful, yet scarce (e.g., Vuilleumier and Simberloff 1980, Recher and Holmes 1985, Holmes 1986, Wiens 1989). In this study, I examined the extent of spatial variation of an assemblage of forest-interior insectivorous birds associated with the *Pohlylepis* community, a unique vegetation association of the high Andes, using the conventional guild approach (i.e., guild classification, number of guilds, and component bird species diversity and abundance). I describe variation in bird species composition and abundance for each foraging guild across twelve *Pohlylepis* woodlands

distributed along 600 km in the Peruvian Andes in light of variation of food resources (available arthropods) and biological interactions (i.e., potential competition). I chose availability in food resources because birds in *Polylepis* woodlands depend on arthropods for foraging and thus fluctuations in availability of food resources could be a limiting factor. I considered arthropods to be limited due to the low temperature, high radiation, dryness, and other environmental variables characteristic of high elevation forests. I assess the relative importance of resource availability in assemblage structure by measuring arthropod abundance in microhabitats where birds' forage (arthropods seem to be attached to protected microhabitats such as the layers of bark) and its relationship with bird species composition and abundance within and across guilds.

Bird species in the *Polylepis* system co-occur with different sets of species within its range of distribution, in particular among regions of study. As species composition changes, so too does the precise nature of species interactions (MacArthur and Wilson 1967, Whittaker 1972). Studies on several taxa have shown that competitive interactions can alter community structure (e.g., rodents, Luo and Fox 1995; Orthoptera, Beckerman 2000; ants, Holldobler and Wilson 1990). The outcome of "natural experiments" has been largely debated (Connor and Simberloff 1979, Diamond and Gilpin 1982), but has led to the search of other analytical procedures such as null model tests (Gotelli 2000, Gotelli and Entsminger 2001). I compared the niche overlap of observed and randomly generated assemblages using null models to determine if structural patterns are consistent with competition theory (Gotelli and Graves 2003).

Although, competition and food resources available are not mutually exclusive factors (Martin 1985, Kotler and Holt 1989), I hypothesize that availability of food resources is of

primary importance to determine bird assemblage structure in the *Polylepis* system (“food resources-hypothesis”). I expect that a) bird species richness and abundance within guilds will follow the patterns of abundance in food resources within microhabitats across *Polylepis* woodlands, and b) that niche overlap in the bird assemblage will be significantly larger than expected by chance. However, if bird species richness and abundance within guilds follow the patterns of abundance in food resources, and niche overlap in the bird assemblage is significantly lower than expected by chance, I will interpret it as the result of present interspecific competition (i.e., species in the assemblage are segregating due to competitive exclusion)(“competition-hypothesis”). In addition if bird species richness and abundance within guilds do not follow the patterns of abundance in food resources and niche overlap in the assemblage is higher than expected by chance, could be interpreted as assemblage instability (i.e., no competitive exclusion is present where it is expected to occur), or that other factors, not assessed in the study, are more important in structuring the bird assemblage.

METHODS

The study system

Throughout the Peruvian Andes above 3500 m elevation, scattered *Polylepis* woodlands are typically found close to streams or forming small patches in gorges on slopes and cliff-edges, where they are surrounded by grasslands. The *Polylepis* community (defined here as the group of organisms with broad taxonomic affinities that occur together and interact within a framework of horizontal and vertical linkages, Giller and Gee 1987) is a distinctive biological system characterized by high levels of endemism (Fjeldså and Krabbe

1990, Fjeldså 1992a, b, c, 1993). The scattered distribution of *Polylepis* woodlands throughout the Andes provides discrete units of study. For this study I selected four *Polylepis* woodlands (> 50 ha) above 3500 m within each of three regions of the Peruvian Andes: Cordillera Blanca, C. Occidental, and C. Vilcanota (see Chapter I and II for description). From north to south the 12 sites selected for the present study and the dominant *Polylepis* tree species occurring at each woodland were: 1) C. Blanca: Aquilpo and Ishinca (*P. weberbauerii*), Morococha and Llanganuco (*P. sericea*); 2) C. Occidental: Yauí and Quichas (*P. weberbauerii*), Maticuna and Japani (*P. incana*); and 3) C. Vilcanota: Yanacocha, Sacsamonte, Pumahuanca, and Quenuamonte (*P. racemosa*). In each forest, I obtained data (i.e., bird species diversity and abundance; food resource abundance) in two replicate sets of four 100 x 10 m transects placed 50 m apart from each other. The last transect from the first set was separated by at least 500 m from the first transect of the second set (see study design in Chapter II).

The bird assemblage

In the Andes of Peru approximately 35-40 bird species are found associated with the *Polylepis* community. The avian assemblage in this community is composed approximately of 28 % frugivorous (species that mainly consume fruit, seeds, and flowers), 20 % nectarivorous (species that mainly consume nectar), 2 % carnivorous (species that mainly consume vertebrates), and 50 % insectivorous (species that mainly consume insects and other arthropods) bird species (Fjeldså 1992, Fjeldså and Krabbe 1990, Fjeldså 1993, Herzog 2003). I included forest interior insectivorous species as representatives of the avian assemblage because they constitute ca. 80 % of the species that regularly breed and winter in *Polylepis* woodlands (“core species”, Remsen 1994). In addition, insectivorous birds associated with the

Polylepis community seem to be “stable” in terms of richness and abundance across seasons when compared to frugivorous or nectarivorous (Herzog 2003) As some of the species in the assemblage migrate or have very low occurrences, gathering enough foraging information on all species is not possible and, therefore, I restricted the analyses to 10 core species: *Oreomanes fraseri*, *Cranioleuca baroni* (replaced in the south by *C. albicapilla*), *Leptasthenura pileata* (replaced in the south by *L. xenothorax*), *L. yanacensis*, *Xenodacnis parina*, *Anairetes alpinus*, *A. nigrocristatus* (clustered together with *A. parulus* because of few observations for both), *Mecocerculus leucophrys*, *Octhoeca rufipectoralis*, and *O. oenanthoides*.

Foraging observations.- I made observations of actively foraging birds at each *Polylepis* forest throughout the day using focal animal sampling (Altman 1974) on core species. I systematically covered transects and moved from one foraging bird to another. I obtained observations from 10 individuals/species for each *Polylepis* forest. Continuous observations were divided into 60-second sequences, in which I tallied the number of microhabitats (e.g., *Polylepis* bark or foliage) and maneuvers (e.g., glean, probe) used by each bird. I used the foraging repertoire (25 categories from core-species) in Bray Curtis ordination (PC-ORD Version 4, McCune and Mefford 1999) and selected Sorensen’s percent dissimilarity as a measure of distance between points (individual birds), variance regression for end point selection, and Euclidean distance for axis projection geometry (Beals 1984, Greig-Smith 1983, McCune and Mefford 1999). In all cases, individual observations falling closer together in the ordination were assumed to belong to the same foraging group. I nominated groups based on the main foraging category used (e.g., foliage gleaners, bark gleaners). At each *Polylepis* forest, I tested for differences among foraging groups using hierarchical Multivariate Analyses of Variance (SPSS Release 12.0) using the scores along the first two ordination axes of all

individuals by species as indicators of the gradient in 'spatial variation' where the species occur. For each axis, species were nested within nominated guilds (using individuals as replicates) and guilds nested within forest. When individuals of the same species fell into two different groups, I used majority rules to decide guild membership (e.g., Holmes et al. 1979, Landres and MacMahon 1980, 1983, Sabo 1980, Sabo and Holmes 1983). The analysis was followed by post-hoc Tukey test (SPSS Release 12.0) to determine if species assigned to groups were more similar in foraging categories used (i.e., not significantly different at $P < 0.01$) than species assign to different groups in all *Polylepis* woodlands.

Assemblage structure

I measured two components of assemblage structure, diversity and abundance of birds within and across foraging guilds. I conducted bird censuses between 0600 and 0800 hrs and 1500 to 1700 hrs, for four consecutive days in 1997 and six days in 1998. Censuses were made by walking transects at a steady pace (ca. 1 km/hr) recording all birds heard and seen (cf. Blake et al. 1994), supplemented by casual observations. I counted the total number of species (i.e., richness) and the number of individuals per species (i.e., abundance), and calculated bird species diversity across woodlands using rarefaction curves (Hurlbert 1971, Sanders 1968) in the Program EcoSim 7.72 (Gotelli and Entsminger 1997-2005) to control for differences in bird abundance while comparing richness across sites. The process was simulated 1000 times specifying the number of individuals that are randomly drawn from each sample. I compared the diversity across *Polylepis* woodlands using the same abundance level (30 individuals) in all cases. I tested for significant differences in total bird abundance

among and within guilds across *Polylepis* woodlands, using hierarchical MANOVA, followed by Tukey's test for post-hoc comparisons.

The potential role of food resource abundance and competition

Food resources.- I measured food resources available to birds by counting arthropods in samples taken from five discrete microhabitats where birds were observed to forage: *Polylepis* bark; *Polylepis*, *Gynoxys*, and *Tristerix* foliage; and moss (see design in Chapter II). I excluded arthropods with less than 2 mm length, individuals with aposematic coloration, or taxa with low occurrence (< 5 individuals per microhabitat), as they are unlikely to be prey for foraging birds due to low acceptability or detectability (Wolda 1990, Servat 1995). I analyzed data on arthropod abundance using hierarchical MANOVA (SPSS Release 12.0) followed by Tukey's to test for differences in arthropod abundance within microhabitats, and microhabitats within *Polylepis* woodlands.

Competition.- To assess the role that competition may be playing in the system, I compared the observed niche overlap of bird species in the assemblage with those generated from null models using Pianka's Index in the EcoSim Program Version 7.72 (Gotelli and Entsminger 1997-2005). Comparisons of observed and randomly generated niche overlaps in assemblages reveal if structural patterns are consistent with competition theory. If observed patterns were not different from randomly generated communities then it will indicate no evidence for competition. However, if different and in the predicted direction (less overlap than expected), this will indicate consistency with competition theory. To construct the null model, I made a matrix of all potential competitor species (i.e., all species that belonged to the same guilds) (rows) by forest (columns). Cell values within each row of the observed matrix

were reassigned without replacement, and mean niche overlap, which is based on comparisons of all possible species pairs, was calculated during each run using RA3 algorithm (Gotelli and Graves 1996). The RA3 algorithm takes into account observed values (e.g., proportional use of microhabitats) and because values are randomly reassigned to different categories by rows, the rows of the utilization matrix are simply reshuffled, and the null model effectively retains observed niche breadth values for each species (Gotelli and Graves 1996). This procedure was repeated 1000 times to provide an overall mean and standard deviation of niche overlap values that could be compared to observed values.

To determine if patterns of bird diversity and abundance within guilds across woodlands was related to variation in food resources, I used Mantel test (PCORD Version 4.10, 1995-1999). For the models, I built pair wise-site distance matrices based on bird diversity and abundance within guilds (response variable) at each forest, and food resource abundance in microhabitats (predictor variable) to evaluate the null hypothesis of no relationship in distance matrices. I used Sorensen's dissimilarity index as a distance measure and performed 999 permutations of the original matrix to determine the significance probability of the observed relationship between the response and predictor variables.

RESULTS

Assemblage structure

Forest-independent ordinations of bird species in the assemblage (based on similarities in foraging categories used by individuals) revealed three to four foraging groups across *Polylepis* woodlands (Fig. 3.1). Overall, the farthest points along the first axis of the

ordination separated individuals that glean or probe proportionally more in *Polylepis* bark, from those that glean proportionally more in *Polylepis* or *Gynoxys* foliage (Fig. 3.1, Appendix 3.1). In the second axis the farthest points separated individuals that capture prey “in the air” (i.e., hawking, hovering, or sally-gleaning) from foliage and bark foragers (Fig. 3.1, Appendix 3.1). Based on the general patterns just described, I named guilds as: “*Polylepis* bark foragers”, mostly conformed by individuals of *Oreomanes fraseri* and *Cranioleuca baroni*/*C. albicapilla*, the “foliage foragers” that included most individuals of *Leptasthenura pileata*/*L. xenothorax*, *L. yanacensis*, and *Xenodacnis parina*, the “aerial hawkers” included most individuals of *Mecocerculus leucophrys*, *Anairetes alpinus*, *A. parulus*/*A. nigrocristatus* (usually found in the canopy); and the “aerial sit and sally gleaners” composed by most individuals of *Octoeca rufipectoralis* and *O. oenantoides* (both of which are usually found in the understory).

Foraging position of individuals (along the two axes of the ordination) within same guild was not significant different ($P > 0.05$) across *Polylepis* woodlands. However, when comparing different guilds at each site, significant differences were detected in all *Polylepis* woodlands as revealed by hierarchical MANOVA tests (Table 3.2), revealing groups of species that differed in the use of the “foraging space”. Moreover, after post-hoc tests, I found that individuals of some species were consistently attached to a particular foraging guild (e.g., *O. fraseri*), while others were highly variable (e.g., *X. parina* and *C. baroni/albicapilla*) (Table 3.2). The inconsistency of some species across forests may result in some of the within-guild variance found across *Polylepis* woodlands (Table 3.2).

Diversity and abundance of insectivorous birds

Overall diversity of insectivorous bird species varied across *Pohlylepis* woodlands, as revealed by rarefaction curves (Fig. 3.2). When number of individuals is controlled for (i.e., 50 individuals in Fig. 3.2) diversity was substantially higher in Aquilpo, Ishinca (C. Blanca), Yanacocha, Sacsamonte and Pumahuanca (C. Vilcanota). On the other side, diversity was lower in Japani, Quichas (C. Occidental), and Quenuamonte (C. Vilcanota) (Fig. 3.2), suggesting that diversity of birds associated with the *Pohlylepis* system varies regionally.

Bird abundance (number of individuals/guild) among guilds was significantly different in all *Pohlylepis* woodlands (MANOVA $F_{3,128} = 23.93$, $P < 0.001$). Nonetheless, when abundance of birds within same guilds was compared across woodlands, no differences were found in bark foragers ($F_{11,12} = 1.24$, $P = 0.356$), foliage foragers ($F_{16,19} = 0.91$, $P = 0.570$), hawkers ($F_{6,41} = 1.19$, $P = 0.326$), or salliers ($F_{8,15} = 2.07$, $P = 0.106$) (Fig. 3.4).

The relative importance of competitive interactions and food resources in assemblage structure

Assemblages did not seem to be structured by competition, as revealed by null models of niche overlap. In all models I found higher foraging overlap than expected by chance, significantly so in 6 forests (Table 3.4), a predicted result for assemblages not structured by competition.

Food resources abundance (arthropods) differed significantly across *Pohlylepis* woodlands within and among microhabitats. I found significant differences in arthropod abundance in moss (ANOVA $F_{11,12} = 9.58$, $P < 0.0001$), *Pohlylepis* bark (ANOVA $F_{11,12} = 5.64$, $P = 0.003$), *Pohlylepis* foliage (ANOVA $F_{11,12} = 20.11$, $P < 0.0001$), and *Gynoxys* foliage

(ANOVA $F_{10,11} = 2.73$, $P = 0.05$) across sites, but not in *Tristerix* foliage ($P = 0.69$). Basically, moss, *Pohlylepis* bark, and *Pohlylepis* foliage contributed most to these differences.

The relative importance of food resources in bird species richness and abundance assessed by Mantel tests; shows a direct and positive relationship between pair-wise site similarities in abundance and richness of birds in the assemblage and pair-wise site similarities in food resources ($r^2 = 0.43$ and $r^2 = 0.33$ respectively, $P < 0.001$, $n = 66$ pairs), which supports predictions of the “local food resources hypothesis”.

DISCUSSION

Foraging guilds identities (i.e., *Pohlylepis* bark foragers, foliage foragers, aerial foragers) were present and largely consistent in most *Pohlylepis* woodlands. However, bird species identities and its abundance at each guild were not necessarily similar across forests, which may be due in part to regional differences in insectivorous bird species diversity and intrapopulation variation in foraging ecology (Chapter II).

High overlap among species in the avian assemblage across *Pohlylepis* woodlands suggests that competitive interactions do not support the classic scenario expected by competition theory (Hutchinson 1957, MacArthur and MacArthur 1961, Urban and Smith 1989), a result supported by several studies based on field observations or assessed through null models in other communities (e.g., Inger and Colwell 1977, Vitt and Caldwell 1994, Vitt and Zani 1998, 1996). The considerable overlap found in bird assemblages of *Pohlylepis* woodlands, suggests that species may be able to coexist through other mechanisms (e.g., microhabitat or prey differentiation) (Hofer et al. 2000). Nonetheless, in the present study

some aspects of competition may have not been detected (e.g., diffuse competition, interference competition).

The role of food resource abundance in bird assemblage structure

Site similarities in species abundance across woodlands were related to site similarities in food resources available, suggesting that birds are able to “track” food resources, or that bird species converge in using food resources in the only microhabitats available (Pianka 1980, Jaksic 1981, Wiens 1983, 1989, Bradley y Bradley 1985).

Abundance and predictable resources may play a major role in structuring the assemblage of birds associated with the *Polylepsis* community. Some foraging microhabitats were more predictable (e.g., *Polylepsis* bark and foliage) than others (e.g., *Tristerix* or *Gynoxys* foliage), so bird species adapted to exploit resources in unpredictable microhabitats were absent (*C. baroni* in Japan) or switch microhabitats (e.g., *X. parina*). However, without complementary experimental manipulations, the relative role of food resources (and competition) influencing present-day community structure can not be unambiguously determined.

Present distribution of *Polylepsis* woodlands (e.g., isolation and habitat extent) suggests an important role for history as a determinant of present day assemblage structure (e.g., Askins et al. 1987, Balent and Courtiade 1992, Lescourret and Genard 1994, Daniels et al. 1992). One of the major determinants of change in recent earth history was cyclic changes in climate and topography during the Pleistocene (Shackleton et al. 1990, and Hooghiemstra and Ran 1994). Many Cordilleras in Peru were covered by ice repeatedly over the last 2-3 million years, which may have restricted species to lower elevations on the Andean slopes, and to

certain mountain basins that remained ice-free (Simpson 1975, Simpson and Todzia 1990, Fjeldså and Kessler 1996). The iced-covered mountain caps may have isolated some refuges with *Polylepis* woodlands from the continuous band of humid shrubbery that is thought to have remained along the Andes. Isolation during glaciations may have promoted species differentiation, remaining endemic to their area of origin (Fjeldså and Kessler 1996). These relict populations that survived periods of global climatic change likely were the source pool of species for colonization of other areas as the glaciers receded (Simpson and Todzia 1990, Fjeldså et al. 1999). In addition, *Polylepis* woodlands disrupted by tectonics and erosion may have become isolated by barriers (e.g., Apurímac Canyon). Dispersal during interglacial periods and post-glacial periods could have been an important influence in explaining present bird composition patterns (Simpson 1975, Fjeldså and Kessler 1996).

Ecological research traditionally has focused on intra-community patterns, especially on the role of competition and other species interactions in community structure (Symstad et al. 2000; Caddle and Greene 1993; Cornell and Lawton 1992; Latham and Ricklefs 1993; Francis and Currie 1998; Huston 1999); and few systematic, quantitative, spatial scale descriptions have been done. Descriptive studies on a large spatial scale, acknowledge the complexity of communities as a dynamic collection of species integrated to varying degrees by numerous factors (ecological and historical) and highlight the likely factors that generate patterns and the scale at which future field studies should be conducted.

This study highlights the importance of considering the spatial scale in the interpretation of patterns of assemblage structure (Levin 1992). In the *Polylepis* community, bird assemblages at local scales appear non-random, with birds separating into distinct guilds. However, at larger scales one sees that the identities and species richness, but not abundance

in guilds vary. Conclusions derived from one or a few sites in this system would likely fail to unravel the relative importance that local factors play in assemblage structure in the *Polylepis* system. Moreover, incorporating the spatial variation in guild composition to assess similarities in functioning is of great importance, because any relationship between diversity and community processes may be driven by functional redundancy or by diversity of species having different functional roles.

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Figure 3.1. Arrangement of individuals along the first and second axes from Bray Curtis ordination (based on 25 foraging categories used by birds) of each *Polylepis* forest. Symbols in the same color represent individuals of the same bird species. Enclosed in circles are groups of individuals similar in foraging. Discontinuous circles include individuals which may not be attached to a particular guild.

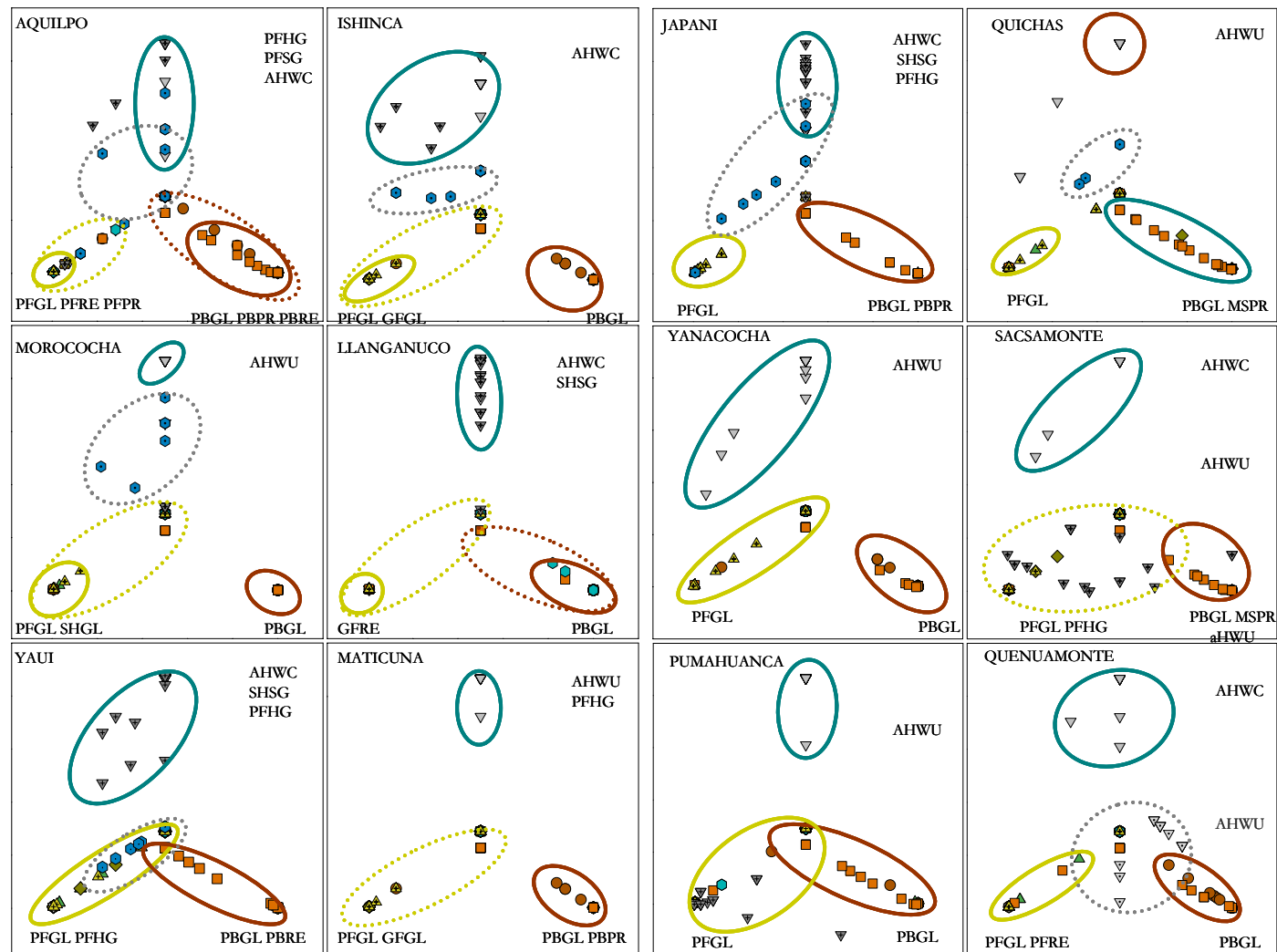


Figure 3.2. Bird species richness (mean \pm SD) in assemblages, as a function of sample size compared by rarefaction curves (EcoSim Program Version 7.72; Gotelli and Entsminger 1997-2005). The reference line indicates bird diversity across *Polylepis* woodlands when the same number of individuals ($n = 30$) is compared (see text).

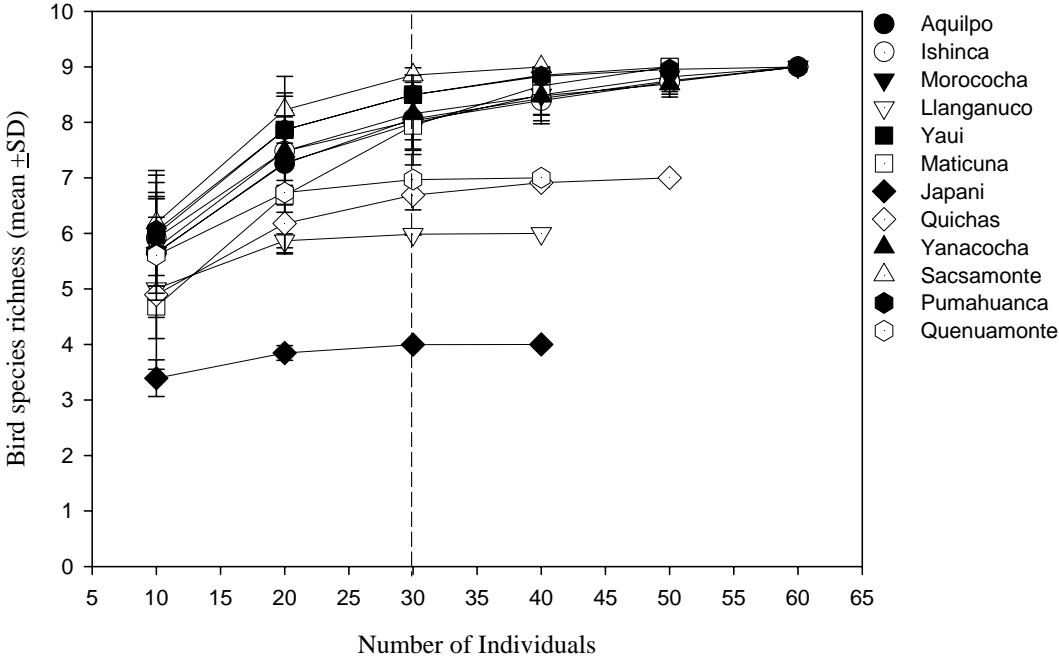


Figure 3.3. Bird abundance among guilds in *Polylepis* woodlands.

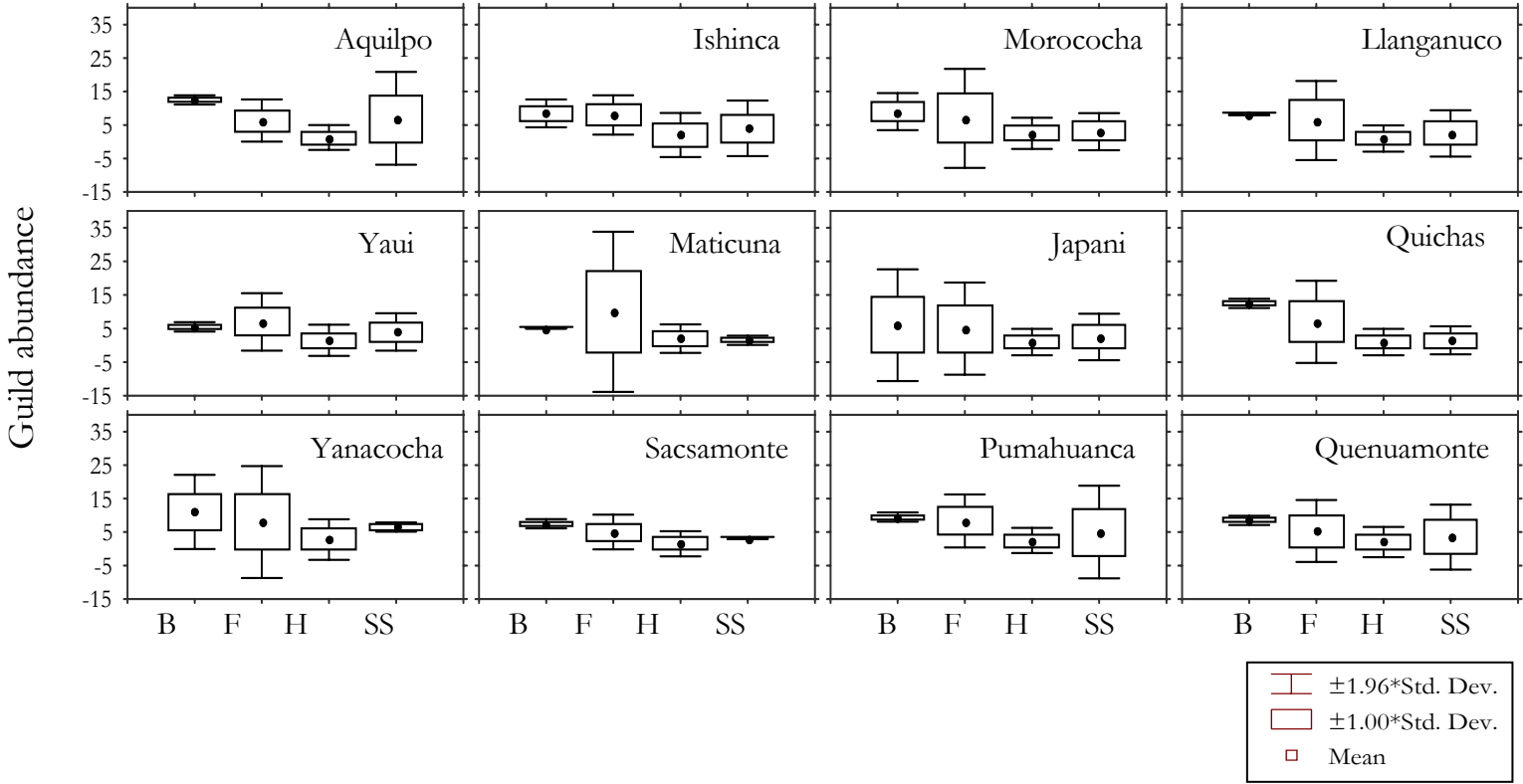
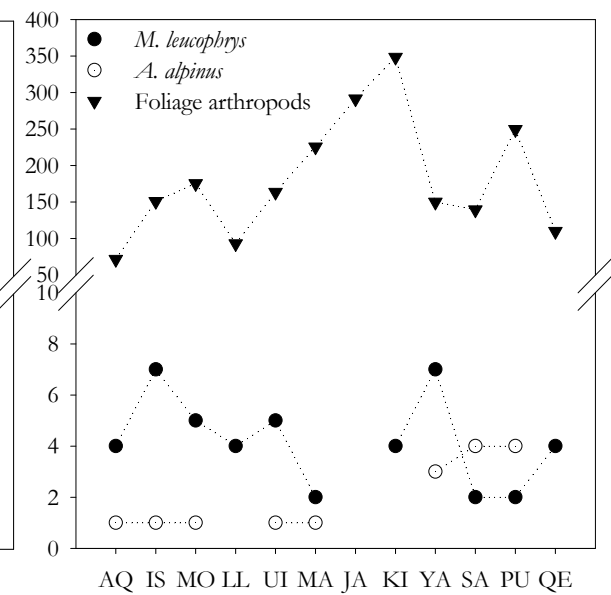
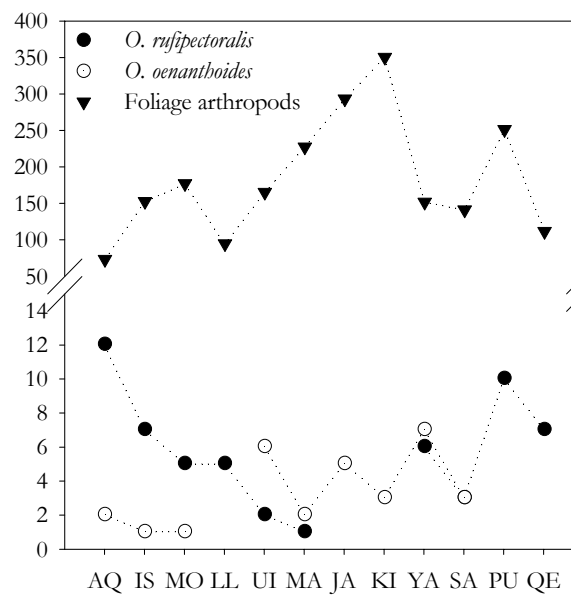
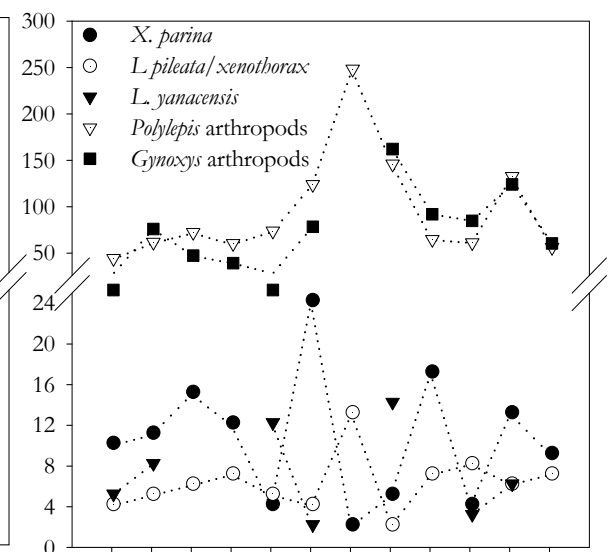
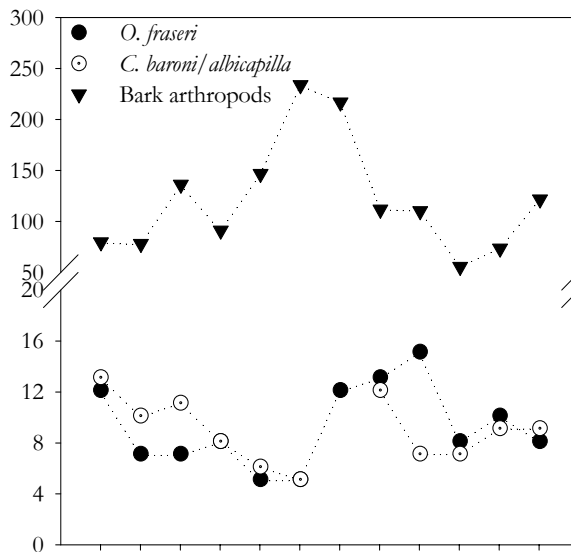


Figure 3.4. Abundance of bird species and total arthropod abundance (= food resources) in associated microhabitats across *Polylepis* woodlands. Each figure groups bird species associated with a particular guild.



AQ IS MO LL UI MA JA KI YA SA PU QE

AQ IS MO LL UI MA JA KI YA SA PU QE

Table 3.1. Species number in avian assemblages of insectivore forest-interior birds associated with *Polylepis* woodlands. Data on abundance fills the cells of the table (See text for details). (1)

Forests: 1 = Aquilpo, 2 = Ishinca, 3 = Morococho, 4 = Llanganuco, 5 = Yauí, 6 =

Maticuna, 7 = Japaní, 8 = Quichas, 9 = Yanacocha, 10 = Sacsamonte, 11 = Pumahuanca,

12 = Quenuamonte. (2) Abundance: C = Common, U = Uncommon, R = Rare.

Family	Species	Regions											
		C. Blanca				C. Occidental				C. Vilcanota			
		1	2	3	4	5	6	7	8	9	10	11	12
Furnariidae	<i>Leptasthenura yanacensis</i>	U	C	NP	NP	C	C	NP	C	NP	U	U	NP
	<i>L. xenothorax</i>	NP	NP	NP	NP	NP	NP	NP	NP	C	C	C	C
	<i>L. pileata</i>	U	U	C	U	U	C	C	U	NP	NP	NP	NP
	<i>Craniolenca albicapilla</i>	NP	NP	NP	NP	NP	NP	NP	NP	C	C	C	C
	<i>C. baroni</i>	C	C	C	C	U	C	NP	C	NP	NP	NP	NP
Tyrannidae	<i>Mecocerculus leucophrys</i>	C	C	U	U	C	R	NP	U	U	R	U	R
	<i>Anairetes alpinus</i>	U	U	NP	NP	R	R	NP	NP	U	R	U	R
	<i>A. parulus</i>	NP	NP	NP	NP	NP	NP	NP	NP	U	NP	NP	U
	<i>A. nigrocristatus</i>	NP	NP	U	NP	NP	NP	NP	NP	NP	NP	NP	NP
	<i>A. reguloides</i>	NP	C	U	C	NP	U	U	NP	NP	NP	NP	NP
	<i>Ochoeca rufipectoralis</i>	C	U	C	C	U	R	NP	NP	C	U	C	C
	<i>O. oenanthoides</i>	U	U	U	NP	C	R	C	U	U	U	NP	NP
Emberizidae	<i>Oreomanes fraseri</i>	U	C	U	C	U	U	C	C	C	C	C	C
	<i>Xenodacnis parina</i>	C	C	C	C	U	U	R	U	C	C	C	C
Insectivore total species number		9	10	9	7	9	10	5	7	9	9	8	8

Table 3.2. Foraging guilds (mean \pm SD) across *Polylepis* woodlands. Hierarchical *MANOVA* tests scores of individuals in each guild along the two first axes in the ordination nested within woodlands. NP = not present.

Forests	Guilds position (mean \pm SD)				Axis 1			Axis 2			MANOVA Pillai's trace		
	Bark	Foliage	Hawkers	Salliers	F	df	P _{value}	F	df	P _{value}	F	df	P _{value}
Aquilpo	6.25 \pm 1.327	3.14 \pm 0.709	1.25 \pm 1.327	3.50 \pm 1.327	13.13	9, 166	.000	20.98	9, 166	.000	17.15	18, 332	.000
Ishinca	4.25 \pm 1.327	3.00 \pm 0.709	2.00 \pm 1.327	NP	22.53	9, 168	.000	79.41	9, 168	.000	37.19	18, 336	.000
Morococho	4.50 \pm 1.327	4.00 \pm 0.839	NP	1.50 \pm 1.327	21.91	8, 150	.000	45.17	8, 150	.000	31.45	16, 300	.000
Llanganuco	4.00 \pm 1.327	3.00 \pm 0.766	2.00 \pm 1.877	2.50 \pm 1.877	46.74	7, 149	.000	34.52	7, 149	.000	41.09	14, 298	.000
Yauí	2.75 \pm 1.327	3.50 \pm 0.938	1.50 \pm 1.327	2.00 \pm 1.327	19.93	8, 151	.000	86.82	8, 151	.000	38.05	16, 302	.000
Maticuna	2.50 \pm 1.327	3.50 \pm 0.839	NP	0.75 \pm 1.327	41.36	7, 137	.000	89.47	7, 137	.000	55.10	14, 274	.000
Japani	6.00 \pm 1.877	3.13 \pm 0.938	NP	2.50 \pm 1.877	42.17	4, 87	.000	72.59	4, 87	.000	48.39	8, 174	.000
Quichas	6.25 \pm 1.327	2.88 \pm 0.938	NP	1.50 \pm 1.877	11.15	6, 117	.000	49.77	6, 117	.000	26.05	12, 234	.000
Yanacocha	5.50 \pm 1.327	4.50 \pm 0.938	1.83 \pm 1.084	3.25 \pm 1.327	8.39	8, 146	.000	66.91	8, 146	.000	22.50	16, 292	.000
Sacsamonte	3.75 \pm 1.327	2.60 \pm 0.839	1.50 \pm 1.327	1.50 \pm 1.327	9.23	7, 152	.000	38.05	7, 152	.000	19.67	14, 304	.000
Pumahuanca	4.75 \pm 1.327	3.60 \pm 0.839	NP	5.00 \pm 1.877	2.19	7, 152	.000	78.50	7, 152	.000	17.20	14, 304	.000
Quenuamonte	4.25 \pm 1.327	2.50 \pm 0.938	NP	3.50 \pm 1.877	33.61	6, 128	.000	93.57	6, 128	.000	49.22	12, 256	.000

Table 3.3. Observed and simulated niche overlap values based on foraging categories used by species in avian assemblages. The mean (\pm SD) of simulated niche overlap for each forest was calculated after 1000 iterations using the *EcoSim* Program, Version 7.72 (Gotelli and Entsminger 1997-2005). I ran the program using randomization algorithm 3 (RA3), and retaining the niche breadth and zero values from original matrix (see text).

Forest	Niche Overlap*		P _{value} (O > E)**
	Observed $X \pm SD$	Simulated $X \pm SD$	
<i>Aquilpo</i>	0.25 \pm 0.051	0.12 \pm 0.030	0.018
<i>Ishinca</i>	0.21 \pm 0.056	0.14 \pm 0.032	0.016
<i>Morococha</i>	0.16 \pm 0.045	0.14 \pm 0.036	NS
<i>Llanganuco</i>	0.24 \pm 0.063	0.15 \pm 0.041	0.050
<i>Yauri</i>	0.15 \pm 0.046	0.12 \pm 0.035	NS
<i>Maticuna</i>	0.21 \pm 0.074	0.14 \pm 0.039	0.015
<i>Japani</i>	0.23 \pm 0.063	0.16 \pm 0.035	NS
<i>Quichas</i>	0.17 \pm 0.021	0.14 \pm 0.032	NS
<i>Yanacocha</i>	0.19 \pm 0.046	0.13 \pm 0.030	0.050
<i>Sacsamonte</i>	0.22 \pm 0.043	0.15 \pm 0.038	NS
<i>Pumahuanca</i>	0.22 \pm 0.045	0.13 \pm 0.037	NS
<i>Quenuamonte</i>	0.18 \pm 0.060	0.13 \pm 0.030	0.030

Appendix 3.1. Scores (high and low) of foraging categories (in bold) along the first and second axes of Bray Curtis ordination for each *Polylepis* woodland. A) AQ = Aquilpo, IS = Ishinca, MO = Morococho, LL = Llanganuco, UI= Yauí, MA = Maticuna, JA = Japari, KI = Quichas, YA = Yanacocho, SA = Sacsamonte, PU = Pumahuanca, QE = Quenuamonte. PBGL = *Polylepis* bark gleaning, PBPR = *Polylepis* bark probe, PFPR = *Polylepis* foliage probe, PFGL = *Polylepis* foliage gleaning, GFGL = *Gynoxys* foliage gleaning, AHWC = aerial hawkers in canopy. NP = Not present. B) PBGL = *Polylepis* bark gleaning, PFGL = *Polylepis* foliage gleaning, PFHG = *Polylepis* foliage hover-glean, MSPR = moss probing, ASSU = aerial sally sit in understory, AHWC = aerial hawkers in canopy. NP = Not present

Foraging substrates		Categories Axis 1	AQ	IS	MO	LL	UI	MA	JA	KI	YA	SA	PU	QE	
BARK	<i>Polylepis</i>	PBGL*	0.870	0.988	1.000	0.994	0.989	0.984	0.903	0.500	0.500	0.500	0.494	0.500	
		PBPR	0.724	0.500	0.500	0.534	0.520	0.601	0.921	0.500	0.500	0.500	0.500	0.500	
		PBHG	0.500	0.683	0.500	0.500	0.458	0.534	0.558	0.500	0.400	0.500	0.500	0.500	
		PBRE	0.811	0.500	0.500	NP	0.700	0.500	NP	0.500	0.500	NP	0.500	0.500	
	Others	DBPR	0.571	0.624	0.500	0.500	0.500	0.500	0.500	NP	NP	0.500	0.500	0.500	0.500
		DBGL	0.500	NP	NP	NP	0.500	0.500	NP	NP	NP	0.500	0.500	0.500	NP
GBGL		0.500	0.500	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	
FOLIAGE	<i>Polylepis</i>	PFGL	0.113	0.058	0.023	0.016	0.046	0.018	0.019	0.074	0.076	0.947	0.987	0.045	
		PFSG	0.452	0.436	0.500	0.508	0.379	0.486	0.455	0.500	0.637	0.514	0.500	0.662	
		PFHG	0.476	0.500	0.500	0.497	0.032	0.334	0.500	0.375	0.671	0.282	0.232	0.557	
		PFRE	0.170	0.215	0.158	0.436	NP	0.301	0.115	0.500	0.359	0.575	0.500	0.056	
		PFPR	0.167	0.205	0.500	NP	NP	NP	NP	NP	NP	0.500	0.740	0.075	
		PFIG	0.500	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	0.242	
	<i>Gynoxys</i>	GFGL	0.346	0.427	0.423	0.235	0.500	0.050	0.144	NP	0.500	0.516	0.500	0.500	
		GFHG	0.500	NP	NP	0.500	NP	0.461	0.500	NP	0.512	NP	0.500	0.642	
		GFRE	0.500	0.500	0.500	0.042	0.500	NP	NP	NP	0.500	0.500	0.500	0.500	
	Moss	MSPR	NP	0.500	NP	NP	NP	0.500	0.500	0.500	0.500	0.500	NP	0.500	
	<i>Tristerix</i>	TRGL	NP	NP	NP	NP	0.500	NP	NP	0.214	NP	NP	NP	NP	
		TRRE	NP	NP	NP	NP	0.418	NP	NP	0.411	NP	NP	NP	NP	
	Shrubs	SHGL	0.500	0.500	0.442	0.490	0.455	NP	0.500	0.480	0.444	NP	NP	0.719	
		SHSG	0.391	0.419	0.468	0.500	0.350	0.457	0.500	0.500	0.681	NP	NP	0.547	
	GROUND		GRSA	0.483	0.409	0.446	NP	0.493	NP	0.420	0.330	0.281	NP	0.500	0.500
GRGL			NP	NP	NP	NP	NP	NP	NP	NP	0.500	NP	NP	NP	
AIR		ASSU	0.420	0.499	0.497	0.524	0.467	0.494	0.434	0.462	0.489	0.500	0.531	0.527	
		AHWC	0.402	0.479	0.500	0.490	0.477	0.485	0.500	0.962	0.911	0.103	0.034	0.923	

Foraging substrate		Categories Axis 2	AQ	IS	MO	LL	UI	MA	JA	KI	YA	SA	PU	QE
BARK	<i>Polylepis</i>	PBGL*	0.295	0.407	0.052	0.037	0.033	0.009	0.056	0.479	0.500	0.486	0.844	0.928
		PBPR	0.344	0.482	0.317	0.289	0.295	0.230	0.046	0.479	0.500	0.486	0.407	0.518
		PBHG	0.420	0.454	0.338	0.405	0.404	0.269	0.606	0.479	0.400	0.486	0.303	0.633
		PBRE	0.315	0.482	0.317	NP	0.051	0.289	NP	0.566	0.500	NP	0.292	0.696
	Others	DBPR	0.389	0.463	0.317	0.307	0.307	0.289	NP	NP	0.500	0.486	0.292	0.533
		DBGL	0.420	NP	NP	NP	0.307	0.289	NP	NP	0.500	0.486	0.292	NP
		GBGL	0.420	0.482	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP
FOLIAGE	<i>Polylepis</i>	PFGL	0.277	0.380	0.051	0.029	0.074	0.015	0.015	0.103	0.137	0.128	0.008	0.105
		PFSG	0.797	0.530	0.683	0.338	0.249	0.718	0.510	0.479	0.299	0.518	0.292	0.326
		PFHG	0.740	0.482	0.317	0.736	0.051	0.358	0.677	0.373	0.182	0.176	0.072	0.367
		PFRE	0.326	0.475	0.227	0.388	NP	0.182	0.066	0.479	0.281	0.420	0.292	0.111
		PFPR	0.230	0.329	0.317	NP	NP	NP	NP	NP	NP	0.486	0.292	0.116
		PFPG	0.420	NP	NP	NP	NP	NP	NP	NP	NP	NP	0.292	0.188
	<i>Gynoxys</i>	GFGL	0.131	0.021	0.244	0.379	0.307	0.029	0.083	NP	0.500	0.468	0.292	0.452
		GFHG	0.420	NP	NP	0.672	NP	0.266	0.657	NP	0.449	NP	NP	0.279
		GFRE	0.209	0.337	0.317	-0.006	0.307	NP	NP	NP	0.500	0.486	0.155	0.452
	Moss	MSPR	NP	0.482	NP	NP	NP	0.249	0.289	0.980	0.500	0.486	NP	0.452
	<i>Tristerix</i>	TRGI	NP	NP	NP	NP	0.307	NP	NP	0.512	0.125	NP	NP	NP
		TRRE	NP	NP	NP	NP	0.262	NP	NP	0.451	NP	NP	NP	NP
	Shrubs	SHGL	0.420	0.482	0.057	0.349	0.283	NP	0.458	0.462	0.426	NP	0.274	0.282
		SHSG	0.392	0.453	0.539	0.750	0.571	0.405	0.673	0.479	0.313	NP	NP	0.394
	GROUND		GRSA	0.555	0.425	0.530	NP	0.303	NP	0.378	0.335	0.325	NP	NP
GRGL			NP	NP	NP	NP	NP	NP	NP	0.479	NP	NP	NP	NP
AIR		ASSU	0.528	0.481	0.827	0.325	0.293	0.797	0.420	0.447	0.963	0.981	0.037	0.423
		AHWC	0.753	0.965	0.326	0.784	0.848	0.520	0.739	0.104	0.129	0.212	0.436	0.124

