# DIVERSITY AND ABUNDANCE OF ORCHIDS IN A PERUVIAN CLOUD FOREST

Rebecca Repasky Luke[1]
*Department of Biology*
*Texas Christian University*
*TCU Box 298930*
*Fort Worth, Texas 76129, U.S.A.*

John P. Janovec
*Botanical Research Institute of Texas*
*500 East 4th St.*
*Fort Worth, Texas 76102-4060, U.S.A.*
*jjanovec@brit.org*

Eric Christenson
*4503 21st Ave West*
*Bradenton, Florida 34209, U.S.A.*

John E. Pinder III[2]
*Department of Biology*
*Texas Christian University*
*TCU Box 298930*
*Fort Worth, Texas 76129, U.S.A.*

Keri McNew Barfield
*Botanical Research Institute of Texas*
*500 East 4th St.*
*Fort Worth, Texas 76102-4060, U.S.A.*

## ABSTRACT

Although there is considerable diversity among the orchids of the Peruvian cloud forests, there is little quantitative data on species abundances and distributions. Most information is limited to local species lists, which have sometimes been incomplete and sometimes based on varying taxonomic sources. This study, which lasted from September 2005 until August, 2006, was designed to provide a comprehensive assessment of orchid diversity and abundances within a 560-ha cloud forest reserve northwest of Cusco. It involved intensive monthly collections of flowering orchids to assess biodiversity and monthly analyses of orchid diversity, abundances, and flower phenologies in 47 permanent, 5m by 5 m plots. Monthly collections identified 239 morphospecies within the 560 ha reserve with 130 of these identified as previously named species. Of the 239 morphospecies, only nine could be termed abundant based on their occurrence in more than 1/3 of the permanent plots or their mean density being > 2 individuals / m$^2$. There was little apparent overlap in species composition of the orchid flora at this site with those observed in similar studies at Machu Picchu and Manu National Park sites. Moreover, few of the nine abundant orchid species were abundant or even present at other sites. Although communality, formation of a species community, among abundant neotropical tree species has been suggested for broadly dispersed sites in western Amazonia, this study found little evidence of a similar communality in the orchid flora of these Peruvian cloud forests.

Key Words: Orchidaceae; Andes; cloud forests; diversity; abundance; phenology; Wayqecha Biological Field Station

## RESUMEN

Aunque hay una diversidad considerable entre las orquídeas de las nefosilvas[3] peruanas, hay pocos datos cuantitativos sobre las abundancias y distribuciones de las especies. La mayor parte de la información está limitada a listas especies locales, que a veces son incompletas y a veces basadas en fuentes taxonómicas heterogéneas. Este estudio, que se desarrolló de Septiembre de 2005 a Agosto de 2006, fue diseñado para hacer una valoración exhaustiva de la diversidad y abundancia de orquídeas en una reserva de nefosilva de 560-ha en el noroeste de Cusco e implicó colecciones intensivas mensuales de orquídeas en flor para valorar la diversidad análisis mensuales de la diversidad de orquídeas, abundancias y fenología floral en 47 parcelas permanentes de 5m por 5 m. En las colecciones mensuales se identificaron 239 morfoespecies en las 560 ha de reserva con 130 de estas identificadas como especies nombradas previamente. De las 239 morfoespecies, sólo nueve pudieron ser calificadas como abundantes basándonos en su aparición en más de 1/3 de las parcelas permanentes o su densidad media > 2 individuos / m$^2$. Hubo poco solapamiento aparente en la composición de especies de la flora orquidológica de este lugar con la observada en estudios similares en Machu Pichu y en el Parque Nacional de Manu. Más aún, pocas de las nueve especies de orquídeas eran abundantes o estaban presentes en los otros sitios. Aunque entre especies arbóreas neotropicales se ha sugerido que son comunes para zonas amplias el oeste de Amazonia, Este estudio encontró pocas pruebas de un comportamienteo similar en la flora orquidológica de estas nefosilvas peruanas.

The Orchidaceae is one of the largest families of flowering plants (Stebbins 1981; Gentry 1988; Gravendeel et al. 2004) with at least 1,000 mostly epiphytic species occurring in Peru alone (Iblish et al. 1996). The high Peruvian species diversity of orchids, especially that of epiphytic orchids in Andean cloud forests, has been recognized and explored for years. A common orchid from the Peruvian Andes, *Epidendrum secundum*,

[1] Current Address: 4428 Calmont Ave., Fort Worth, Texas, 76107.
[2] Current Address: Department of Environmental and Radiological Health Sciences, Colorado State University, 305 W Magnolia, PMB 231, Fort Collins, CO, 80521.
[3] Se propone el término nefosilva para designar los bosques que se desarrollan en lugares de niebla (en inglés *cloud forest*). Las dos partes que componen la palabra ya se usan en el lenguaje científico.

was first characterized in 1760 (Rolfe 1916). In 1911, Hiram Bingham described the Machu Picchu site and commented on the orchids occurring there (Christenson 2003). This high orchid diversity occurs due to a mixture of conditions including (1) a cool, moist climate favorable to epiphytes, (2) the diversification of isolated populations on separate mountain ranges (Tremblay et al. 2005), and (3) the ability of orchid species to easily hybridize (Tremblay et al. 2005).

Although this diversity has been recognized, there is limited quantitative information on the species richness and spatial distribution of orchids across sites and along elevation gradients in the Peruvian Andes. More is known about how these factors affect epiphytes in general than orchids in particular. These montane forests harbor a high diversity and abundance of epiphytic plant species (Grubb et al. 1963; Cornelissen & Ter Steege 1989) with maximum species richness and endemism occurring in wet aseasonal forests on fertile soils at elevations of 1500 to 2000 masl (Gentry & Dodson 1987; Iblish et al. 1996; Kessler, 2002; Kuper et al. 2004; van der Werff & Cosiglio 2004; Kromer et al. 2005). Species richness declines above 2000 m asl but whether this decline indicates some climatic optimum or merely reflects the decline in available land mass above this elevation remains unclear (Kromer et al. 2005). Orchid diversity generally follows the trends for all epiphytes (Kessler 2002; Kuper et al. 2004; Kromer et al. 2005), but the pattern may vary among orchid genera (Kessler 2002).

Detailed studies of orchid diversity and distribution at cloud forest elevations are limited to two studies in southeastern Peru. One was a 12-month study in a 143.5-hectare section on the Machu Picchu Historical Sanctuary (MPHS) near the Winay-Wayna structures (WW; Zambrano et al. 2003a). The other was a 12-month inventory of 16 100-$m^2$ plots in the Manu National Park (MNP; Zambrano et al. 2003b). Both studies report more than 170 orchid species, with limited overlap with the extensive species list compiled by numerous investigations at the MPHS (Christenson 2003). These two studies suggest a diverse orchid flora composed of numerous species that may have limited spatial distributions. Although these studies document high species diversity at each site and high site-to-site variability in species composition, neither study assesses the relative abundances of the various orchid species. Comparison of the variability in species compositions among these studies is also complicated by potential problems in nomenclature that are difficult to resolve because of the lack of access to reference specimens, digital imagery, or detailed collection data.

The present extent of our understanding of Andean orchid diversity is similar to those that existed for western Amazonian tree floras before the advent of quantitative studies of species abundances. Based on early compilations of species lists at different sites, the forests could be depicted as small-scale mosaics of relatively unpredictable species composition. As quantitative studies were performed following the recommendations of Phillips and Raven (1996) and others, patterns of structure involving some widely dispersed, commonly occurring, and relatively abundant taxa could be recognized (Pitman et al. 2001; Macia & Svenning 2005). Although some studies have not provided strong support for the existence of such widespread communality, formation of a species community, of abundant tree species (e.g., Phillips et al. 2003; Tuomisto et al. 2003; Vormisto et al. 2004), they have demonstrated that testing for the presence, or the absence, of such communality requires abundance as well as species composition be documented.

This study had two main goals. First, to initiate quantitative assessments of orchid diversity and abundance in cloud forests similar to those employed for Amazonian tree flora, and second to compare the results to other detailed studies of cloud forest orchid diversity in southeastern Peru to determine possible communalities in abundant taxa. The specific objectives of the study were to: (1) determine orchid species richness; (2) estimate the relative abundances of species; and (3) question whether the abundant orchid species at this site were also abundant, or at least present, at other research sites in the region. In addition, data were obtained to assess the effects of elevation and different habitats on patterns of local orchid diversity and abundance. If elevations and habitats have large effects, they could contribute to heterogeneity in species compositions and abundances.

## METHODS

The design of this study emulates the general protocols recommended by Phillips and Raven (1996) for assessing tree diversity in the Neotropics. These protocols share procedures designed to quantify diversity on a local scale by obtaining: (1) a more complete inventory of plant species composition; (2) an assessment of the spatial distribution of species; and (3) basic phenological information. These objectives are accomplished by conducting surveys to document the species composition and by monitoring of permanent plots for species abundances. For orchids, these objectives were addressed between September, 2005 and August, 2006 through monthly, systematic collections of the orchid species present and the monthly monitoring of permanent plots to measure diversity, distribution, and abundance of the species present. Because the study involves the application of new protocols to quantify orchid abundance and diversity, an evaluation of these protocols with recommendations for potential modifications are also discussed.

**Study site.**—Research was conducted at the 560-ha Wayqecha Cloud Forest Research Station (WCFR; 13°10'40"S, 71°36'20"W) located 60 km northeast of Cusco in southeastern Peru (Fig. 1). The station borders Manu National Park and is owned and operated by the Amazon Conservation Association (ACA) of Washington, DC and its sister organization in Peru, the Asociación para la Conservación de la Cuenca Amazónica (ACCA). Elevations at WCFR range from 2200 to 3200 m, and the primary natural vegetation is upper montane forest (Young & León 2000). The forest is continually saturated with rain and fog. Temperatures average 11°C with little seasonal variation. Precipitation ranges from < 10 mm in the months of June and July to > 100 mm in the months of January, February, and March.

**Systematic plant collection.**—To document the orchid species occurring at WCFR, approximately 10 days of each month were devoted to collecting, photographing, and preserving specimens of flowering orchids. Every orchid with a unique vegetative or reproductive morphology was considered to be a potential new morphospecies unless it could be positively identified as belonging to a previously collected type. Although this practice resulted in replicate collections of some orchid species, it minimized the number of missed species.

One or more specimens were collected for each potentially new morphospecies. At least one specimen was deposited in the herbarium of the Museo Nacional Mayor de Historia Natural (USM) in Lima, Peru. Another specimen was deposited in the herbarium of the Botanical Research Institute of Texas (BRIT) in Fort Worth, Texas, and additional specimens were dispersed to orchid experts at other herbaria. Flowers were also collected and preserved in 80% alcohol and 20% glycerine and deposited at BRIT.

Each potential morphospecies was assigned an identification number, and pertinent data were recorded including: (1) date of collection; (2) location as determined by a Garmin Map76C global positioning system unit (GPS, nominal accuracy < 15 m); (3) relative flower size (1 to 5, 5 being the largest); (4) color of the flower (particularly lip and column colors); and (5) habit (terrestrial or epiphytic). The habitat of the individual was also classified as: (1) tall cloud forest with tree heights > 15 m; (2) short cloud forest with tree heights < 15 m; and (3) grassy areas with no trees or few trees with heights < 3 m. Grassy areas likely resulted from disturbances, such as logging, road construction, or fire over the past 60 years (Young & León 2000; Lozano et al. 2006). To aid in species identification, ≥8 mega-pixel digital photographs were taken for each potential morphospecies. Collection data and digital photographs are accessible through the Atrium Biodiversity Information System at BRIT (http://atrium.andesamazon.org).

Upon completion of the field collections, specimens of potential morphospecies were compared in the herbarium and judged to be either a unique, valid taxon, or to be conspecific with another collected morphospecies. For those morphospecies judged to be conspecific, the collected specimens were combined into a single morphospecies. All morphospecies collections were reviewed by taxonomic experts to confirm their morphospecies status and to begin the process of species identification and description.

**Quantitative data collection.**—To analyze the effects of elevation and habitat differences on orchid diversity, abundance, and distribution, 47 permanent, 5 × 5 m plots were established across the elevation gradient within WCFR. Because of steep gradients and dense vegetation, the plots were established at ran-

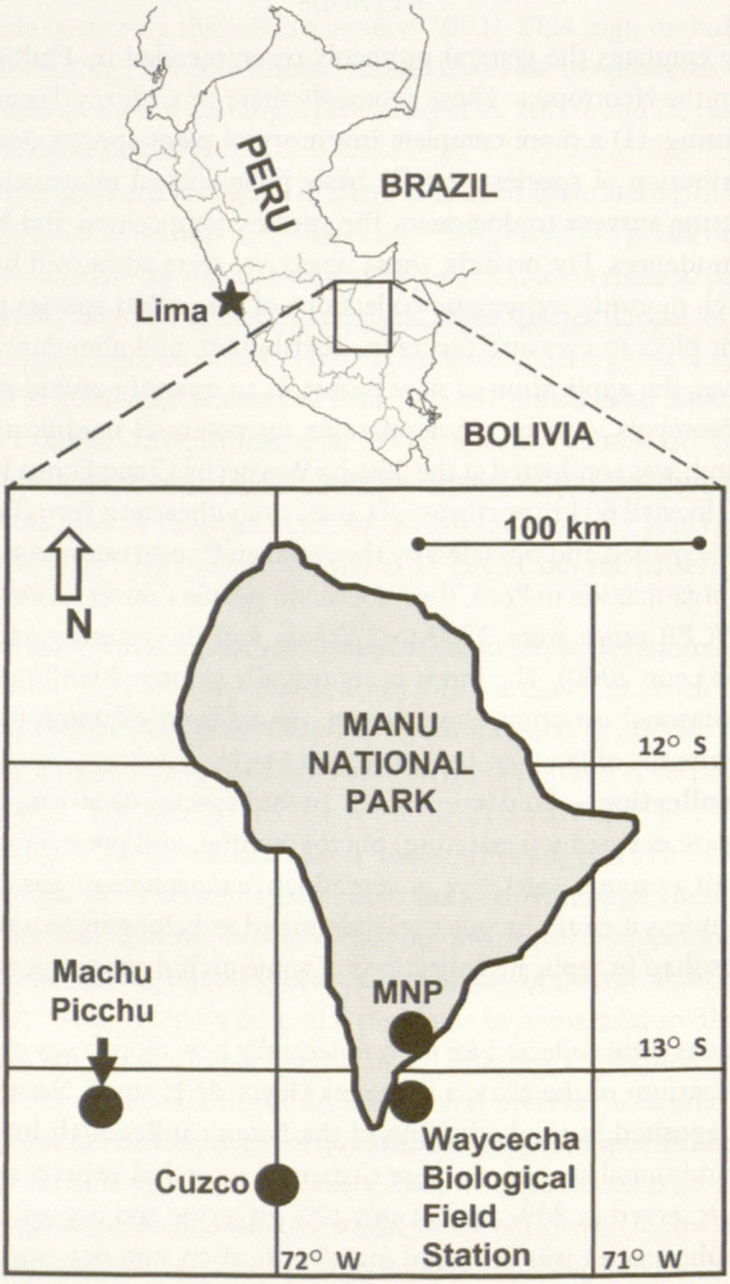


Fig. 1. The location of Wayqecha Biological Field Station (2200–3200 m) in southeastern Peru relative to the city of Cuzco, Machu Picchu, Manu National Park, and the study site of Zambrano et al. (2003b) denoted as MNP within Manu National Park.

dom locations along pre-existing trails passing through the characteristic forest and grassland habitats of the area. The latitude, longitude, and elevation of each plot were measured by GPS. Habitats were classified as tall cloud forest, short cloud forest, or grassy areas, as described above.

From September 2005 through August 2006 the plots were monitored between the 9th and the 13th of each month for the occurrence of potential morphospecies in flower. For the first occurrence of a potential morphospecies in a plot, the species was catalogued using its identification number from the general collection, and the number of individuals with flowers, total number of flowers, and whether the orchid was occurring as a terrestrial or epiphytic form was recorded. If a potential new morphospecies was first encountered in the plots, it was added to the general collection using the previously described procedures to collect suitable specimens located outside of the plot. If the orchid only occurred in the plot, only digital photographs were taken to assist in species identification. For subsequent monthly observations of a morphospecies in a plot, the number of individuals with flowers and the total number of flowers were recorded. General linear model tests of the effects of elevation and habitat type on the species richness and density of orchids were performed using the Statistical Analysis System (SAS; Cody & Smith 2006).

Limited resources and field conditions prevented each individual plant from being tagged, and it is possible that individuals counted as flowering in one month could also be counted as flowering in subsequent months. For this reason, the term density as used in subsequent discussions is a minimum estimate of density taken as the maximum number of individuals of that morphospecies observed flowering in that plot in any one month.

**Rarefaction analysis.**—To evaluate how well the plot sampling could estimate the species richness determined by systematic collections, rarefaction curves (Gotelli & Colwell 2001) were computed using the non-parametric species richness estimators Chao 1 (Chao 1984) and Chao 2 (Chao 1984, 1987). These procedures use the occurrence of rarer species in the samples to adjust the observed number of species for the number of species that were likely missed in the sampling. The Chao 1 procedure defines rareness as being represented by only a few individuals. The Chao 2 procedure defines rareness as being observed in only a few plots. Chao1 and Chao 2 estimators and their 95% CI were computed from 10,000 randomizations of plot sequences using the software EstimateS 8.0 (Colwell 2006). Other richness estimators were also computed and gave comparable results.

## RESULTS

**Systematic collections.**—From the 341 potential morphospecies collected, 239 unique morphospecies were identified from 49 genera. Over 134 morphospecies have been identified as previously described species, and six other are new to science (Christenson & Repasky 2008; Nauray & Galán de Mera 2008). The remaining 102 morphospecies remain to be identified as previously named species or described as species new to science. It is important to note that the as yet unidentified taxa reported here are morphospecies based on structural characteristics which may not be supported by subsequent genetic analysis. However, it is also possible that subsequent genetic analyses may separate apparently similar orchids into separate species. The number of morphospecies per genus ranged from 41 for *Stelis* to < 2 species in 32 other genera. The number of morphospecies in the other common genera *Epidendrum*, *Maxillaria*, and *Pleurothallis* were three, six and nine, respectively. A species list organized by genus is presented in Appendix S1.

Monthly collections were important for adequately assessing orchid diversity as most species flowered for ≤ 3 months. Monthly importance is best illustrated by the flowering phenology data from the plot studies where only six of the 17 species flowering in September 2005 were among the 65 species observed to be flowering in February, 2006. Only six of the 65 species flowering in February were among the 23 species flowering in August, 2006.

**Plot characteristics.**—Plots ranged in elevation from 2496 to 2993 m, and when grouped into equal elevational intervals of 175 m, there were similar numbers of plots in each interval (Fig. 2). All three habitats were present in each interval.

**Orchid densities and distributions.**—The minimum number of individuals recorded in all of the plots for the duration of the study was 2565, which is the sum of the maximum number recorded in any month for a species in each plot. Minimum numbers of individuals per plot showed little variation with elevation or habitat type ($F = 0.33$; df = 5, 41; $P > 0.10$; Appendix S2). Mean (± Standard Deviation; SD) densities for grassy areas, short cloud forest, and tall cloud forest were 2.2 (± 1.1), 2.4 (± 1.2), and 1.9 (± 2.1) individuals per m$^2$, respectively. Densities declined with increasing elevations at a rate of 0.38 individuals per m$^2$ per 100 m of elevation, but this rate was not significantly different from 0. Densities were approximately normally distributed (Kolmogorov-Smirnov test of normality; Conover 1971).

**Distribution of orchid species among plots.**—Only 128 of the 239 species were observed in plots during the 12-month study. Because almost all orchid individuals observed in plots flowered during the study, this underrepresentation was due to inadequate sampling of the spatial heterogeneity of the orchid flora. The number of species per plot ranged from three to twenty-five with a median of nine species per plot. Most of the orchid species (72%) occurred as epiphytes.

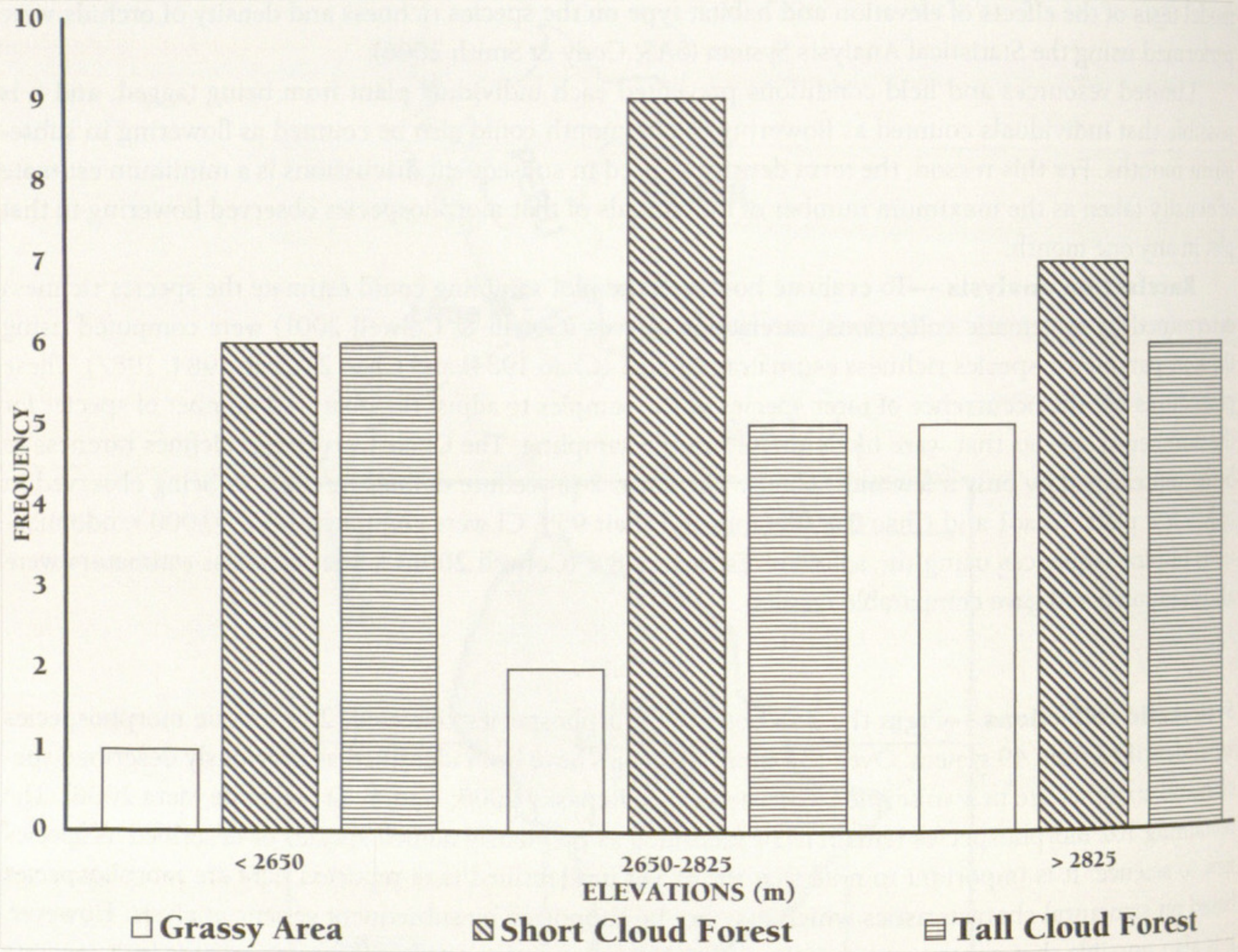


**Fig. 2. The number of plots in each habitat type and elevation interval.**

For terrestrial species, there were significant differences in the number of terrestrial species per plot among habitats ($F = 6.15$; df = 2, 43; $P < 0.01$) and at different elevations ($F = 14.09$; df = 1, 43; $P < 0.01$). The mean (± SD) number of terrestrial species per plot for tall cloud forest was 1.8 (± 2.5). This was significantly ($P < 0.05$) less than the means of 4.0 (± 2.7) species per plot in short cloud forest and 3.4 (± 2.6) species per plot in grassland. There was a decrease of 0.81 (SE = 0.22) terrestrial species per plot for each 100 m increase in elevation. The two terrestrial orchids with the highest frequency of occurrence, *Epidendrum secundum* and *Elleanthus sp.*, occurred in 17 of the 47 plots.

For epiphytic species, there were also significant differences in the number of species per plot among habitats ($F = 7.29$; df = 2, 43; $P < 0.01$) and at different elevations ($F = 19.12$; df = 1, 43; $P < 0.01$). The number of epiphytic species per plot for short cloud forest (10.1 ± 4.5) was significantly greater than that for the tall cloud forest (6.3 ± 3.7) and the grass areas (6.2 ± 4.0). For each 100 m increase in elevation, there was a decrease of 1.4 (SE = 0.3) epiphytic species per plot. The epiphytic orchid with the highest frequency of occurrence was *Pleurothallis acuminata* which occurred in 20 plots.

There was considerable variation among species in abundances and frequencies of occurrence. There were 27 species with an abundance of one individual and 12 species with an abundance of two. The majority of orchid species had mean densities < 2 per m$^2$. Only nine species had mean densities > 2 per m$^2$. These were, listed in order of decreasing abundance, *Pachyphyllum* sp.1, *Pleurothallis* aff. *vestigipetala, Stelis breviracema, Elleanthus* sp. 1, *Stelis grandibracteata, Maxillaria alpestris, Epidenrum secundium, Pleurothallis acuminata* and *Pachyphyllum pectinatum.* Most (77%) species were observed in < 5 plots (Fig. 3). Forty-nine species were found in only one plot, and 22 species occurred in only two plots. Only six species were observed in > 30%

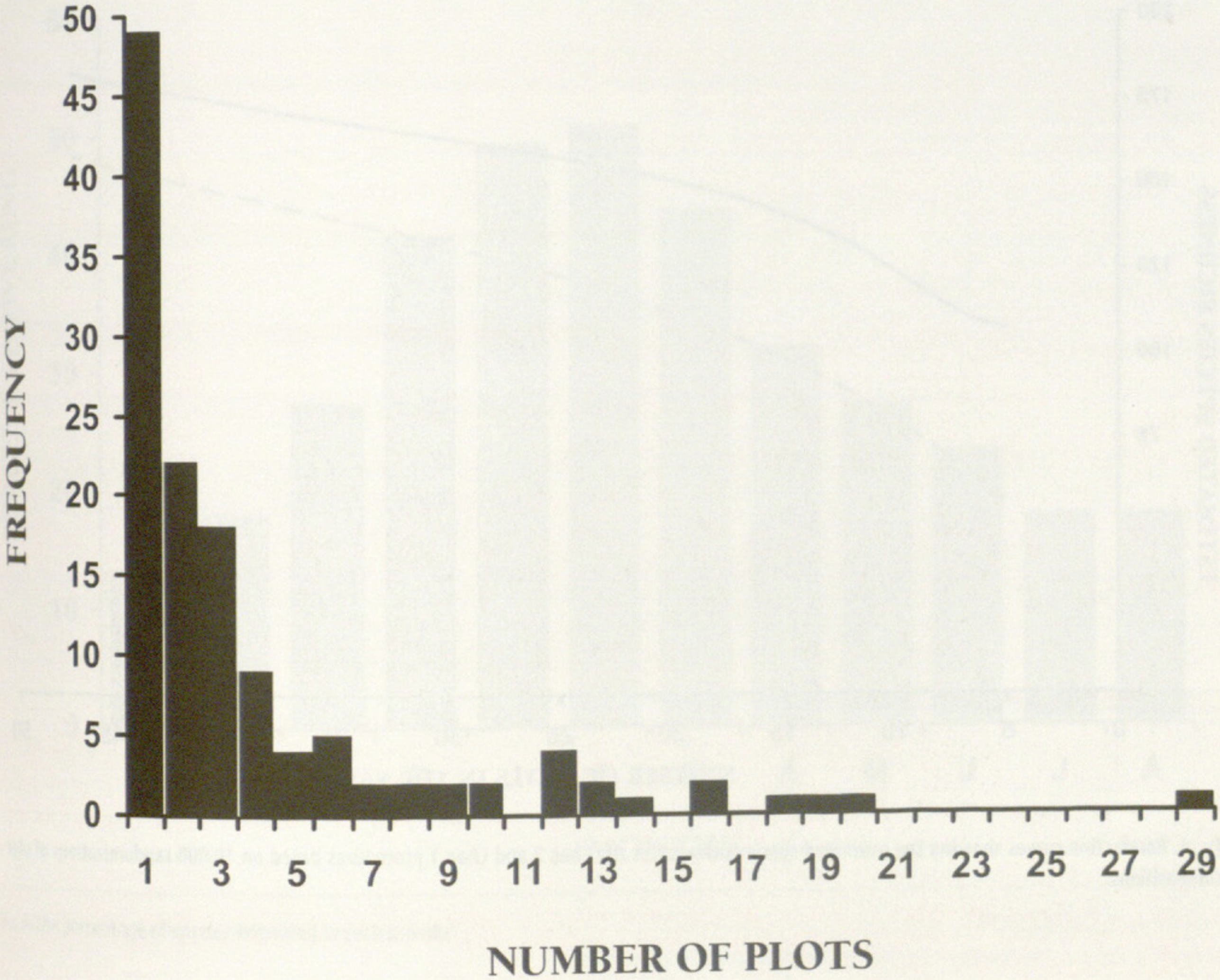


FIG. 3. The number of species occurrences per plot.

of the 10 plots. These, listed in order of decreasing frequencies of occurrence, were *Pachyphyllum* sp. 1, *Pleurothallis acuminata*, *Stelis breviracema*, *Epidendrum secundum*, *Elleanthus* sp. 1, and *Pachyphyllum pectinatum*.

**Rarefaction Analysis.—**Both the Chao 1 and Chao 2 procedures consistently underestimated the species richness of 239 observed in the systematic collections (Fig. 4). The Chao 2 procedure, which defines rareness based on incidences of occurrence, was consistently greater than the Chao 1 procedure, which defines rareness based on the abundance of individuals. The final estimate for the Chao 2 procedure, based on randomizations of all 47 plots, was 183 species with a 95% Confidence Interval (95% CI) of 155 to 240 species. The final estimate for the Chao 1 procedure was 158 species with a 95% CI of 140 to 206 species.

**Flowering Phenology.—**The percent of species in the plots that were in flower ranged from 13% in September to 51% in February (Fig. 5), and there was little differences in percents among habitat types or across elevations. The mean (± SD) density of flowers also ranged from a minimum of 0.65 (± 1.1) per $m^2$ in September to a maximum of 25.7 (± 37.6) per $m^2$ in February. Peak flowering occurred during months with > 100 mm of rainfall, and minimum flowering occurred in months with < 5 mm of rainfall. The median flowering duration was three months, and most (80%) species flowered for less than six months. The proportion of flowering species shared between successive months was ≤ 0.40 (Fig. 6), and there were no pronounced peaks in the proportions shared that indicated major subsets of species exhibiting synchronous flowering.

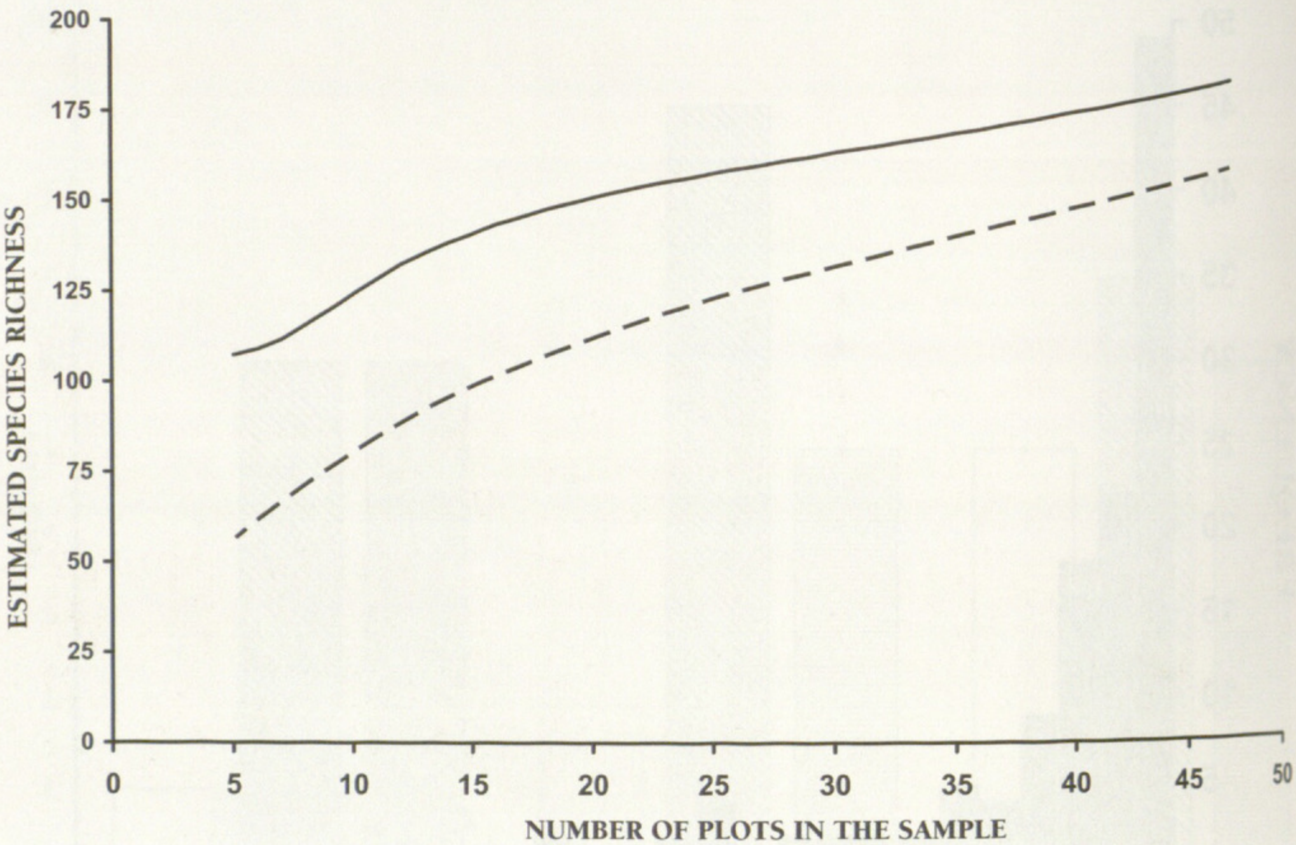


**Fig. 4. Rarefaction curves showing the estimated species richness for the Chao 2 and Chao 1 procedures based on 10,000 randomizations of plot compositions.**

## DISCUSSION

The cloud forests at WCFR harbor a rich diversity of orchids with 130 species and 109 morphospecies, or 239 unique taxa, collected and documented during the 12-month sampling period. Most of the orchids were relatively rare. Over 75% of them were either found only during the systematic collections or only occurred in ≤ 2 of the 47 plots. Those that did occur in plots were often represented by ≤ 3 individuals. Only nine of the species could be described as being abundant due to their occurrence in more than one-third of the plots or their mean densities being > 2 individuals per m$^2$. These included the identified species *Epidendrum secundum*, *Maxillaria alpestris* aff., *Pachyphyllum pectinatum*, *Pleurothallis acuminata*, *Pleurothallis vestigipetala* aff., *Stelis breviracema*, and *Stelis grandibracteata* and the morphospecies *Elleanthus* sp. 1 and *Pachyphyllum* sp. 1. *Elleanthus* sp. 1 and *Epidendrum secundum* were primarily terrestrial species. The *Pachyphyllum* and *Pleurothallis* species were primarily epiphytes. The remaining three abundant species occurred with similar abundances in both terrestrial and epiphytic growth forms.

Similar intensive, 12-month assessments of orchid species richness in the Peruvian Andes have been made near the Winay-Wayna ruins (WW; Zambrano et al. 2003a) at MPHS which is about 100 km west of WCFR and in a small portion of Manu National Park (MNP; Zambrano et al. 2003b) to the northeast of WCFR. In addition to these intensive analyses of smaller sites, Christenson (2003) has compiled a species list for the 35,952-ha MPHS based on collections since that site's discovery in 1911. Comparing the species compositions of these sites and WCFR is complicated because: (1) the MNP and WW studies included orchid species from elevations above and below the cloud forest; (2) a number of unidentified or undescribed morphospecies still exist; and (3) variation in the use of nomenclature and taxonomic classifications among study sites and researchers. Despite these complications, three general trends in species richness and composition are apparent.

First, the intensive studies of small areas have found comparably large numbers of orchid species. There

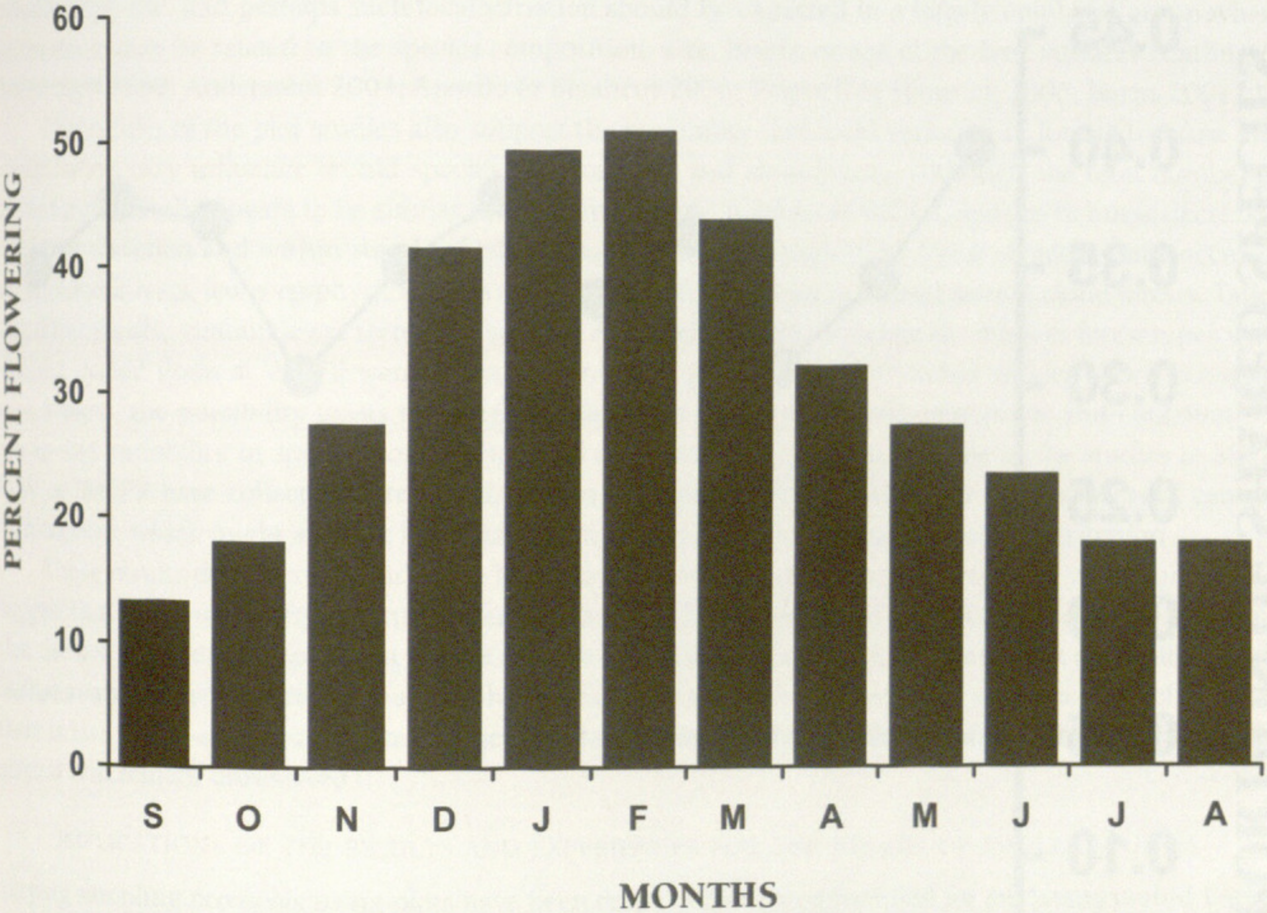


Fig. 5. The percentage of species flowering in each month.

were 212 species found at MNP and 179 at WW. These numbers are similar to the 239 species found at WCFR (Christenson 2003). The number of species at each of these sites is also similar to the 252 that have been reported for all of MPHS. As many as 50 species of epiphytic orchids have been found in 1-ha plots at cloud forest elevations (Kromer et al. 2005).

Second, most of the species occurring at the intensely studied sites belong to the large genera *Epidendrum*, *Maxillaria*, *Pleurothallis* and *Stelis*, but there is variability in the relative importance of these genera among sites. *Epidendrum* is the most numerous genus at the MNP and WW sites, but *Stelis* is the most numerous genus at WCFR. *Epidendrum* is the second most diverse genus at WCFR, but *Stelis* is less diverse than the other three genera at the MNP and WW sites.

Third, although the important genera appear to be similar across sites, the species representing these genera differ among sites. No species list is provided for the WW site, but Zambrano et al. (2003b) listed the 63 species that occurred at MNP which are also known to occur at MPHS. Apparently, the remaining 149 species at MNP could not be matched to MPHS species. Of those 63 species common to MNP and MPHS, only 28 occurred at WCFR. Thirty-six of the 63 species common to MNP and MPHS were members of *Epidendrum*, *Maxillaria*, *Pleurothallis* and *Stelis*, but only 17 of these occurred at WCFR.

There are other differences in species compositions between WCFR and MPHS. Of the 79 genera reported for both WCFR and MPHS (Christenson 2003) only 43 occur at both sites, and 25 of these are represented at WCFR by only a single species. For those genera represented by numerous species at WCFR, there were six *Epidendrum* species, 16 *Maxillaria* species, and six *Pleurothallis* species that are not reported from MPHS. Additional species that occur at WCFR but not at MPHS may be discovered as progress is made on accurate identifications of the numerous morphospecies in the difficult *Stelis*. In addition, a number of WCFR species are new additions to the flora of Peru or previously undescribed species (Christenson & Repasky 2008).

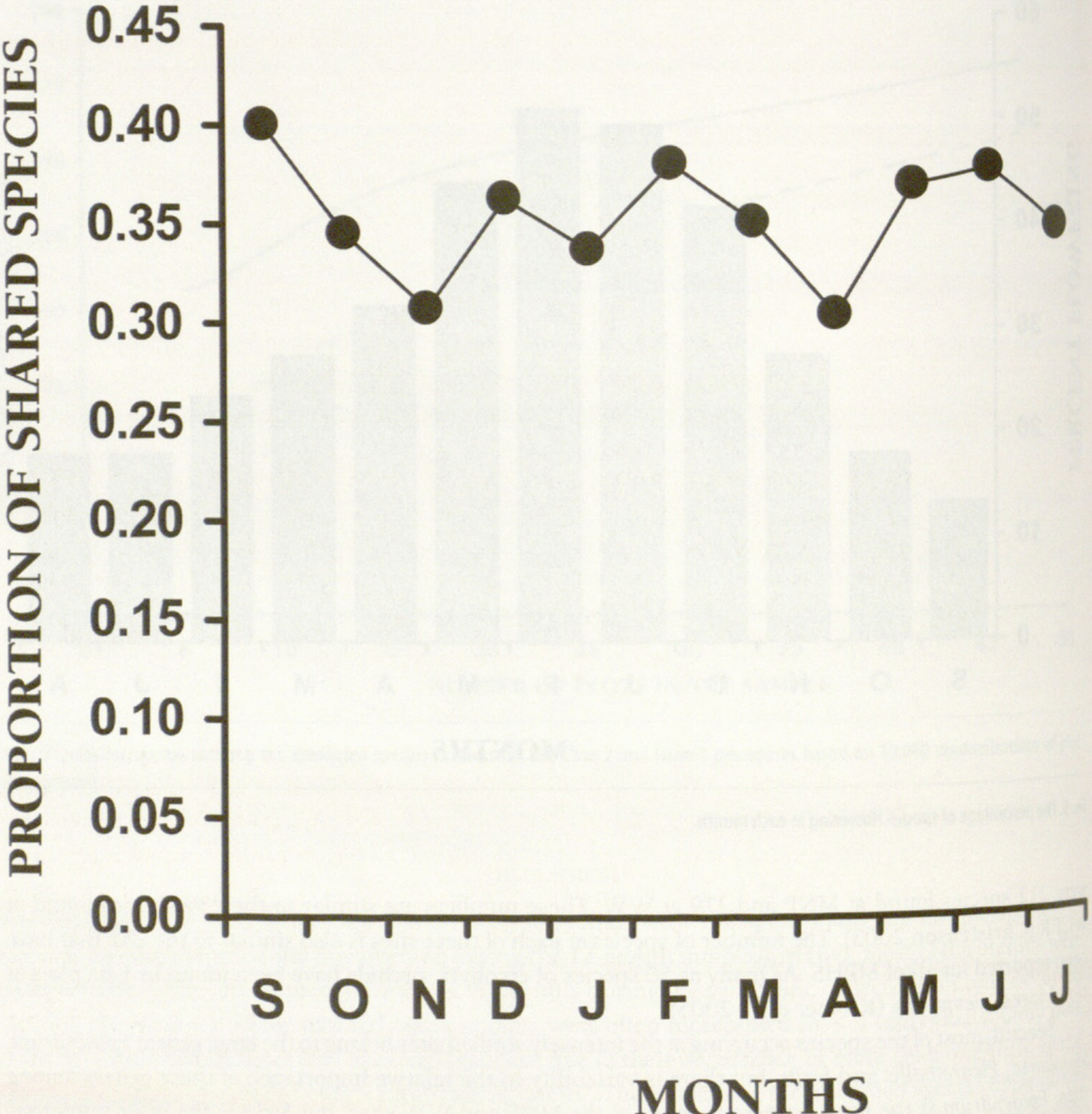


**Fig. 6. The proportions of species flowering in one month that were also flowering in the following month.**

At present, the species lists from MPHS and the sites of intense study are analogous to the early tree species lists for the Amazonian rainforests. They suggest a small-scaled and as yet unpredictable structure of the orchid community. The only quantitative data on abundance which might imply commonalities in structure are from WCFR, and two aspects of these data do not suggest a simple communality among the sites. First, only four of the seven named abundant species at WCFR, *Epidendrum secundum, Maxillaria alpestris, Pachyphyllum pectinatum*, and *Pleurothallis acuminata*, were among the 28 species that are common to WCFR, MNP and MPHS. Second, *Pachyphyllum* sp. 1 and *Elleanthus* sp. 1, two of the abundant species at WCFR, were not readily-identifiable or familiar species. If they were similarly abundant at other sites, it may be expected that they would be among the commonly-known and readily-recognized species.

This lack of correspondence of abundant species among sites implies local variation in the abundant orchid species. Large variation in orchid species composition between sites only kilometers apart has been reported by Kuper et al. (2004) where 70 % of the species occurring at one site are not present at the neighboring site, and perhaps such local variation should be expected in a largely epiphytic group where occurrence may be related to the species composition, size, height or age of the host surfaces (Catling & Lefkovitch 1989; Andersohn 2004; Arevalo & Betancur 2006; Trapnell & Hamrick 2006; Burns 2007).

The results of the plot studies also support the possibility that local variation in forest structure and composition may influence orchid species compositions and abundances. Although the total number of orchid individuals appears to be similar across elevation and habitats at WCFR, species richness decreases at higher elevation and within stands of taller cloud forests. Although more forest structure may occur in taller cloud forests, fewer epiphytic species occur in these forests than in shorter stature cloud forests. Taller cloud forests also contain fewer terrestrial species. Although attempts to relate elevation or forest types with distinct orchid floras at WCFR were obfuscated by the large proportion of orchid species which occurred in < 5 plots, the possibility exists that such orchid-forest flora associations may occur and contribute to site-to-site variability in species composition and abundance. Unfortunately none of the studies at MNP, WW or WCFR have collected or reported data on tree species, tree densities, or other aspects of canopy architecture, which might account for variations in orchid diversity, abundance, and distribution.

These results document considerable local variation in the orchid floras of Peruvian cloud forests and suggest that this level of variation may extend to the abundant members of the flora. There is little evidence that the abundant orchid species at WCFR are also abundant, or perhaps even present, at other sites. Until similar analyses of species richness and orchid abundances are available from other sites, the issue of whether there is less site-to-site variation among the abundant members of the orchid flora than that for the flora in general will remain unresolved.

## IMPLICATIONS OF THE RESULTS AND EXPERIENCES FOR THE DESIGN OF SIMILAR STUDIES

Varying sampling protocols using plots have been employed or recommended for analyzing orchid floras. Zambrano et al. (2003a) used rectangular 25 m$^2$ plots at WW, and Zambrano et al. (2003b) used 2 m × 50 m plots at MNP. Gradstein et al. (2003) suggested 20 m × 20 m plots for sampling the < 10-m tall understory of tropical rain forests. The results and experiences of the present study with 5 m × 5 m plots suggest three potentially useful modifications for studies attempting to determine the species composition, species richness, and relative abundance of cloud forest orchids.

First, plots alone are unlikely to be sufficient to determine the species composition of the study area. Although almost all orchid stems with the plots at WCFR flowered and were assigned to morphospecies, the plots contained less than 60% of the species observed in the systematic collection. Zambrano et al. (2003a) also supplement their plot analyses with orchid collections from the area surrounding the plots. The rarefaction analyses also suggest that plots alone are unlikely to be effective in estimating the total number of species present.

Second, the assessments of species composition and abundance in plots must be performed on a monthly basis. There is too little overlap in species flowering in successive months to permit less frequent sampling. Because a single orchid flower may persist for as few as six to eight days (Tremblay et al. 2006), it is possible that even more frequent than monthly sampling may be required.

Third, the plot design and manner of data collection used here can be modified to reduce disturbance and improve efficiency. It was necessary to enter the 5 m × 5 m plots to assess species types and abundances. Despite care, such intrusion may affect the plots composition through time. A design using a rectangular plot with a width of 2 m would allow data collection with little need for intrusion. Given the large disparity between the abundance of rare and common species, enumerating the exact abundance of individuals in a few plots may not be as informative as assessing relative abundance in many plots. A more rapid assessment of relative abundance using an ordinal scale where, for example, 0 indicates no individuals present, 1 indicates < 3 individuals, 2 indicates 3 to 10 individuals and so forth, would be sufficient to establish a gradient of rare to abundant species. A plot composed of a linear arrangement of five 2 × 2 m subplots with the estimated abundance being the median ordinal score of the five subplots could be more rapidly sampled and could provide sufficiently useful data from more plots in less time.

Potentially 150 or more of these plots composed of five 2 × 2 m subplots could be monitored per month with less effort than was required for the 47 plots of this project. The ordinal data from these linear plots can still be used to assess relative abundance and to estimate total species richness using the incidence-based procedures, such as Chao 2, which only require presence and absence data to assess species rareness and predict the number of unsampled species.

Although more efficient sampling procedures could have been employed, this study demonstrates the importance of using long-term combinations of systematic plant collections and quantitative analyses of permanent plots to assess orchid species occurrences and abundance in the Peruvian Andes. It also demonstrates the limited ability to extrapolate these results to broader scales because of the absence of comparable quantitative data from other sites. Even comparisons of species lists among studies are constrained by the incompletely documented taxonomy of some collections. Hopefully, the widespread dissemination of WCFR collections supplemented by extensive information available on the Atrium web site will facilitate future comparisons and allow a more complete assessment of the degree to which orchid communities may possess communalities in composition and abundance similar to those which appear to be occurring for the diverse forest communities of western Amazonia.

## APPENDIX S1

A list of orchid species collected at Wayqechas Biological Field Station between September 2005 and August 2006. Species listed as unidentified either remain to be classified as a previously described species or described as a potential new species. Additional information including date of collection, flower description, habit, habitat, digital images is located at http://atrium.andesamazon.org/.

| Genera | Named Species | No. of as yet Unidentified Species | Genera | Named Species | No. of as yet Unidentified Species |
|---|---|---|---|---|---|
| 1 Altensteinia | boliviensis | | | roncanum | |
| 2 Barbosella | cucullata | | | saxicola | |
| 3 Baskervilla | machupicchuensis | | | schlimii | |
| 4 Brachionidium | | 1 | | scutella | |
| 5 Cranichis | ciliata | 3 | | secundum | |
| | engelii | | | subliberum | |
| 6 Cyclopogon | | 1 | | syringothyrsus | |
| 7 Cyrtidiorchis | rhomboglossa | | | trachysepalum | |
| 8 Cyrtochilum | cimiciferum | 1 | 12 Erythrodes | | 1 |
| | minax | | 13 Frondaria | caulescens | |
| 9 Dichaea | | 1 | 14 Gomphichis | | 2 |
| 10 Elleanthus | aurantiacus | 3 | 15 Habenaria | corydophora | |
| | capitatus | | | dentifera | |
| | kermesinus | | | uncatiloba | |
| | weberbauerianus | | 16 Hapalorchis | pumilus | |
| 11 Epidendrum | anderssonii | 6 | 17 Hofmeisterella | eumicroscopica | |
| | blepharistes | | 18 Lepanthes | dictyota aff. | 12 |
| | farinosa | | | falcata | |
| | fimbriatum | | | mesochlora | |
| | goodspeedianum | | | ptyxis | |
| | gracillimum | | | pumila | |
| | haenkeanum | | | tracheia cf. | |
| | jajense | | 19 Lepanthopsis | | 1 |
| | laxicaule | | 20 Liparis | elegantula | |
| | macrostachyum aff. | | | retusa | |
| | marcapatense | | 21 Malaxis | | 4 |
| | mesomicron | | 22 Masdevallia | antonii | |
| | renzii | | | picturata | |

| Genera | Named Species | No. of as yet Unidentified Species | Genera | Named Species | No. of as yet Unidentified Species |
|---|---|---|---|---|---|
| 23 Maxillaria | alpestris aff. | 3 | | mesochlora | |
| | brevifolia | | | quadrata | |
| | brunnea | | | rubens | |
| | christobalensis aff. | | | ruberrina | |
| | cuzcoensis | | | vargasii | |
| | deniseae | | | vestigipetala aff. | |
| | dichroma | | 31 Ponthieva | cornuta | |
| | divaricata | | | diptera | |
| | floribunda | | | garayana | |
| | gigantea | | 32 Prescottia | petiolaris | |
| | graminifolia | | | stachyodes | |
| | haemathodes | | 33 Prosthechea | farfanii | |
| | meridensis | | | fusca | |
| | mungoschraderi aff. | | 34 Pterichis | | 1 |
| | notylioglossa | | 35 Rusbyella | caespitosa | 2 |
| | nubigena | | 36 Sauroglossum | | 1 |
| | procurrens | | 37 Scaphyglottis | punctulata | |
| | quitensis | | | summersii | |
| | rotundilabia | | 38 Solenidiopsis | galianoi | |
| | trigona | | 39 Stelis | antennata | 41 |
| | winaywaynaensis | | | breviracema | |
| 24 Myoxanthes | frutex | | | grandibracteata | |
| | gyas | | | tricardium | |
| | hirsuticaulis aff. | | | uninervia | |
| 25 Neodraya | rhodoneura | | 40 Stellilabium | cuscoense | |
| 26 Odontoglossum | digitatum | 1 | 41 Stenoptera | acuta | |
| | machupicchuense | | | ciliaris | |
| | mystacinum | | 42 Sudamerlycaste | cobbiana | |
| | subuligerum | | | gigantea | |
| | tetraplasium | | 43 Telipogon | austroperuvianus | |
| 27 Oncidium | retusum | | | casadevalliae | |
| 28 Pachyphyllum | breviconnatum | 3 | | javiercastroviejoi | |
| | crystallinum | | | mesotropicalis | |
| | ecallosum | | | salinasii | |
| | gracillimum | | | santiagocastroviejoi | |
| | hispidulum | | | tayacajaensis | |
| | pectinatum | | | vargasii | |
| 29 Pityphyllum | laricinum | | | | |
| 30 Pleurothallis | acuminata | 9 | 44 Trichoceros | armillatus | |
| | angustilabia | | 45 Trichosalpinx | arbuscula | 1 |
| | cassidis | | | chamaelepanthes | |
| | cordata | | | intricata | |
| | coriacardia | | | teagueii | |
| | cyathioflora | | 46 Vargasiella | peruviana | |
| | imraei | | 47 Xylobium | elatum | |
| | lamellaris | | | squalens | |
| | melanostele | | 48 Unknown genus | | 1 |

APPENDIX S2

The elevation, habitat type, minimum number of individuals and number of species for 5 m x 5 m plots at the Wayqechas Biological Field Station.

| Plot Number | Elevation above Mean Sea Level (m) | Habitat Type | Minimum Number of Individuals per Plot | Number of Species |
|---|---|---|---|---|
| 1 | 2612 | Short Cloud Forest | 23 | 8 |
| 2 | 2609 | Short Cloud Forest | 48 | 12 |
| 3 | 2575 | Tall Cloud Forest | 9 | 3 |
| 4 | 2557 | Tall Cloud Forest | 52 | 15 |
| 5 | 2530 | Tall Cloud Forest | 107 | 17 |
| 6 | 2508 | Tall Cloud Forest | 67 | 13 |
| 7 | 2496 | Tall Cloud Forest | 28 | 11 |
| 8 | 2517 | Short Cloud Forest | 43 | 15 |
| 9 | 2501 | Grass Areas | 30 | 12 |
| 10 | 2524 | Short Cloud Forest | 66 | 22 |
| 11 | 2538 | Tall Cloud Forest | 19 | 9 |
| 12 | 2526 | Short Cloud Forest | 127 | 25 |
| 13 | 2808 | Tall Cloud Forest | 5 | 3 |
| 14 | 2787 | Short Cloud Forest | 35 | 5 |
| 15 | 2760 | Tall Cloud Forest | 62 | 5 |
| 16 | 2686 | Short Cloud Forest | 63 | 15 |
| 17 | 2662 | Grass Areas | 101 | 19 |
| 18 | 2666 | Short Cloud Forest | 68 | 19 |
| 19 | 2666 | Short Cloud Forest | 78 | 19 |
| 20 | 2665 | Short Cloud Forest | 83 | 24 |
| 21 | 2661 | Short Cloud Forest | 32 | 14 |
| 22 | 2606 | Short Cloud Forest | 63 | 20 |
| 23 | 2982 | Short Cloud Forest | 43 | 9 |
| 24 | 2993 | Short Cloud Forest | 102 | 14 |
| 25 | 2969 | Grass Areas | 59 | 6 |
| 26 | 2973 | Grass Areas | 50 | 7 |
| 27 | 2966 | Grass Areas | 21 | 3 |
| 28 | 2970 | Grass Areas | 32 | 3 |
| 29 | 2968 | Short Cloud Forest | 33 | 6 |
| 30 | 2946 | Short Cloud Forest | 16 | 5 |
| 31 | 2945 | Short Cloud Forest | 52 | 10 |
| 32 | 2954 | Short Cloud Forest | 31 | 9 |
| 33 | 2917 | Tall Cloud Forest | 202 | 3 |
| 34 | 2915 | Tall Cloud Forest | 11 | 7 |
| 35 | 2849 | Short Cloud Forest | 34 | 8 |
| 36 | 2820 | Tall Cloud Forest | 11 | 7 |
| 37 | 2844 | Tall Cloud Forest | 120 | 7 |
| 38 | 2839 | Tall Cloud Forest | 15 | 8 |
| 39 | 2831 | Tall Cloud Forest | 17 | 5 |
| 40 | 2819 | Short Cloud Forest | 90 | 17 |
| 41 | 2817 | Short Cloud Forest | 68 | 12 |
| 42 | 2802 | Grass Areas | 82 | 15 |
| 43 | 2817 | Short Cloud Forest | 103 | 15 |
| 44 | 2801 | Tall Cloud Forest | 12 | 5 |
| 45 | 2778 | Tall Cloud Forest | 45 | 9 |
| 46 | 2845 | Tall Cloud Forest | 37 | 6 |
| 47 | 2932 | Grass Areas | 70 | 8 |

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## REFERENCES

Andersohn, C. 2004. Does tree height determine epiphyte diversity? Selbyana 25:101–117.

Arévalo, R. and J. Betancur. 2006. Vertical distribution of vascular epiphytes in four forest types of the Serranía de Chiribiquete, Colombian Guayana. Selbyana 27:175–185.

Burns, K.C. 2007. Network properties of an epiphyte metacommunity. J. Ecol. 95:1142–1151.

Catling, P.M. and L.P. Lefkovitch. 1989. Associations of vascular epiphytes in a Guatemalan cloud forest. Biotropica 21:35–40.

Chao, A. 1984. Non-parametric estimation of the number of classes in a population. Scand. J. Stat. 11:265–270.

Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. Biometrics 43:783–791.

Christenson, E. 2003. Machu Picchu: Orchids. PROFONAPE, Lima, Peru.

Christenson, E. and R. Repasky. 2008. A new species of *Stellilabium* from southern Peru. Orchid Digest 72:170–172.

Cody, R.P. and J.K. Smith. 2006. Applied statistics and the SAS programming language, Fifth Edition. Pearson Prentice Hall, NJ.

Colwell, R.K. 2006. EstimateS 8.0 User's Guide. http://viceroy.eeb.uconn.edu/estimates.

Conover, W.J. 1971. Practical nonparametric statistics. John Wiley and Sons, Inc. New York.

Cornelissen, J.H.C. and H. Ter Steege. 1989. Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. J. Trop. Ecol. 5:131–150.

Gentry, A.H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. Ann. Missouri Bot. Gard. 75:1–34.

Gentry, A.H. and C.H. Dodson. 1987. Diversity and biogeography of neotropical vascular epiphytes. Ann. Missouri Bot. Gard. 74:205–233.

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

Gradstein, S.R., N.M. Nadkarni, T. Kromer, I. Holz, and N. Noske. 2003. A protocol for rapid and representative sampling of vascular and non-vascular epiphyte diversity of tropical rain forests. Selbyana 24:105–111.

Grubb, P.J., J.R. Lloyd, T.D. Pennington, and T.C. Whitmore. 1963. A comparison of montane and lowland rain forest in Ecuador. I. The forest structure, physiognomy, and floristics. J. Ecol. 51:567–601.

Iblish, P.L., A. Boegner, J. Nieder, and W. Barthlott. 1996. How diverse are neotropical epiphytes? An analysis based on the "Catalogue of the Flower Plants and Gymnosperms of Peru". Ecotropica 2:13–28.

Kessler, M. 2002. The elevational gradient of Andean plant endemism: varying influences of taxon-specific traits and topography at different taxonomic levels. J. Biogeogr. 29:1159–1165.

Kromer, T., M. Kessler, S.R. Gradstein, and A. Acebey. 2005. Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. J. Biogeogr. 32:1799–1809.

Kuper, W., H. Kreft, J. Nieder, N. Koster, and W. Barthlott. 2004. Large-scale diversity patterns of vascular epiphytes in Neotropical montane rain forests. J. Biogeogr. 31:1477–1487.

Lee, S.M. and A. Chao. 1994. Estimating population size via sample coverage for closed capture-recapture models. Biometrics 50:88–97.

Lozano, P., R.W. Bussman, and M. Kueppers. 2006. Landslides as ecosystem disturbance – their implications and importance in Southern Ecuador. Lyonia 9:75–81.

Macia, M.J. and J.-C. Svenning. 2005. Oligarchic dominance in western Amazonian plant communities. J. Trop. Ecol. 21:613–626.

Nauray, W. and A. Galan de Mera. 2008. Ten new species of *Telipogon* (Orchidaceae, Oncidiinae) from southern Peru. Anales Jardin Bot. Madrid 65:73-95.

Phillips, O.L. and P.H. Raven. 1996. A strategy for sampling neotropical forests. In: Gibson, A.C. Neotropical biodiversity and conservation. University of California, Berkeley. Pp. 141–165.

Phillips, O.L., P.N. Vargas, A.L. Monteagudo. A.P. Cruz, M.C. Zans, W.G. Sanchez, M. Yli-Halla, and S. Rose. 2003. Habitat association among Amazonian tree species: a landscape-scale approach. J. Ecol. 91:757–775.

Pitman, N.C.A., J.W. Terborgh, M.R. Silman, P. Núñez V., D.A. Neill, C.E. Cerón, W.A. Palacios, and M. Aulestia. 2001. Dominance and distribution of tree species in upper Amazonian terra firme forests. Ecology 82:2101–2117.

Rolfe, R.A. 1916. IX—*Epidendrum Secundum* and *E. Elongatum*. Bulletin of miscellaneous information 1916: 49–49.

Stebbins, G.L. 1981. Why are there so many species of flowering plants? BioScience 31:573–577.

Trapnell, D.W. and J.L. Hamrick. 2006. Variety of phorophyte species colonized by the neotropical epiphyte, *Laelia rubescens* (Orchidaceae). Selbyana 27:60–64.

Tremblay, R.L., J.D. Ackerman, J.K. Zimmerman, and R.N. Calvo. 2005. Variation in sexual reproduction in orchids and its evolutionary consequences: a spasmodic journey to diversification. Biol. J. Linn. Soc. 84:1–54.

Tremblay, R.L., G. Pomales-Hernandez, and M.L. Mendez-Cintron. 2006. Flower phenology and sexual maturation: Partial protandrous behavior in three species of orchids. Caribbean J. Sci. 42:75–80.

Tuomisto, H., K. Ruokolainen, M. Aguilar, and A. Sarmiento. 2003. Floristic patterns along a 43-km long transect in an Amazonian rain forest. J. Ecol. 91:743–756.

van der Werff, H. and T. Consiglio. 2004. Distribution and conservation significance of flowering plants in Peru. Biodivers. & Conservation 13:1699–1713.

Vormisto, J., J.-C. Svenning, P. Hall, and H. Balslev. 2004. Diversity and dominance in palm (Arecaceae) communities in terra firme forests in the western Amazonian basin. J. Ecol. 92:577–588.

Young, K. and B. León. 2000. Biodiversity conservation in Peru's eastern montane forests. Mountain Res. Developm. 20:208–211.

Zambrano, D.A., N.S. Revilla, and W.N. Huari. 2003. La familia Orchidaceae L. en Wiñay-Wayna, Sanctuario Histórico de Machu Picchu. Lyonia 3:273–282.

Zambrano, D.A., N.S. Revilla, and W.N. Huari. 2003b. Orquídeas del Valle de Cosñipata, Parte Alta de la Reserva de Biósfera del Manu, Cusco – Peru. Lyonia 3:283–290.