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Circular distribution of an epiphytic herb on trees in a subtropical rain forest

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Abstract: The distribution of the endangered epiphytic orchid *Lepanthes eltoroensis* on the bole of trees was investigated in the Yunque National Forest, Puerto Rico. Using circular statistics, we evaluated if there was preference for cardinal position on the bole of trees along two trails (Tradewinds and El Toro). In addition we tested if larger trees had larger population, and if the distribution of the orchids varied between the two walking trails. Orchids were preferentially distributed on the northwestern side of the bole of trees. Moreover, we found no evidence that the size of trees affected the number of individual orchids. This survey suggests that there is a preference for specific cardinal position on trees for the orchid and thus re-location or establishment of new populations should consider this information to maximize survivorship of this rare orchid.

Resumen: Se estudió la distribución de la orquídea epífita y amenazada *Lepanthes eltoroensis* sobre los troncos de los árboles en el Bosque Nacional Yunque, Puerto Rico. Evaluamos si había preferencia por alguna posición cardinal sobre los troncos a lo largo de dos senderos (Tradewinds y El Toro) usando estadística circular. Asimismo, investigamos si los árboles más grandes soportaban poblaciones más grandes y si la distribución de las orquídeas variaban entre los dos senderos. Las orquídeas se distribuyeron preferentemente en el lado noroccidental de los troncos. Además, no encontramos evidencia de que el tamaño de los árboles afectara el número de individuos de la orquídea. Este estudio sugiere que hay una preferencia de la orquídea por una posición cardinal específica sobre los árboles; por la tanto, la reubicación o el establecimiento de nuevas poblaciones debería tomar en cuenta esta información con el fin de maximizar la supervivencia de esta orquídea rara.

Resumo: A distribuição da epífita *Lepanthes eltoroensis* em perigo no tronco de árvores foi investigada na Floresta Natural de Yunque, Porto Rico. Com recurso a estatísticas circulares, avaliou-se se havia preferências pelas posições cardiais no tronco das árvores localizadas ao longo de dois percursos (Tradewinds e El Toro). Adicionalmente foi testado se as maiores árvores apresentavam populações maiores, e se a distribuição das orquídeas variavam entre os dois percursos. Verificou-se que as orquídeas se encontravam preferencialmente distribuídas na superfície norte dos troncos. Além disso não foram encontradas evidências de que o tamanho das árvores afectassem o número individual das orquídeas. Esta prospecção sugeriu que existe uma preferência das orquídeas por um posição cardial específica nas árvores e, assim, a relocalização, ou estabelecimento de novas populações, deve considerar esta informação para maximizar a sobrevivência desta orquídea rara.

Key words: Circular statistics, *Lepanthes eltoroensis,* niche preference, Orchidaceae, Puerto Rico, Yunque National Forest.

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Introduction

In the Caribbean hurricanes cause the downfall of many trees (Frangi & Lugo 1991), some of which are phorophytes for epiphytes. In Puerto Rico the endangered species *Lepanthes eltoroensis* is a small epiphyte found almost exclusively on the lower part of the bole of trees in the Yunque National Forest. A survey posterior to hurricane Georges showed that 24% of trees with the rare orchid had been felled. We evaluated the effect of relocating individuals from felled to standing trees along two walking trails after hurricane Georges (Tremblay 2008). These experiments have shown that individual survivorship of relocated plants was high but variable among sites chosen for relocation (Benítez-Joubert & Tremblay 2003; Tremblay 2008). In order to maximize the likelihood of survivorship posterior to re-locating plants from fallen trees a survey was conducted to evaluate the most likely sites for re-introduction of species in its native habitat. One of the possibilities that could explain such variation in growth and survivorship among relocation sites is the environmental differences among sites (Catling *et al.* 1986; Catling & Lefkovitch 1989) and the cardinal direction on the trees where plants were relocated. Traditionally, studies investigating the epiphyte distribution have evaluated the spatial distribution across trees or the vertical structure on the individual trees (Freiberg 1996; Nieder *et al.* 2000; Zimmerman & Olmstead 1992). In this study, we evaluate the circular distribution of epiphyte around the bole of trees. We evaluated and determined (1) if there was preference for specific cardinal position around the bole of the tree, (2) if trees of varying size had equal orchid population size, and (3) if the orchid distribution around the bole of the trees varied between the two surveyed trails from a series of natural populations of the orchid *Lepanthes eltoroensis.*

Materials and methods

The model system and data collecting

Lepanthes eltoroensis Stimson is an epiphyte endemic to Puerto Rico, restricted to mountain ridges along the El Toro and Tradewinds trails and the Cerro El Cacique in the Yunque National Forest (YNF). For the purpose of this study, a population is defined as the set of individuals growing on a single phorophyte (i.e., host tree). The orchid *L. eltoroensis* is limited in distribution to the Yunque National Forest and protected by federal law. *Lepanthes eltoroensis* plants are caespitose and prostrate with slender stems, with a solitary leaf (up to 3.8 cm long) subtending one to two inflorescences capable of producing many minute flowers (< 8 mm, Ackerman 1995). Plants are obligate cross-pollinated and protandrous (Tremblay *et al.* 2006). Reproductive success in this orchid as in most orchids is pollinator-limited (Tremblay *et al.* 2005). Previous studies have shown that gene flow (measured by protein electrophoresis) among groups of individuals on trees is limited even when plants are in close proximity and below levels which suggest possibility of independent evolution at the tree level (Tremblay & Ackerman 2001), which is typical of many orchids (Tremblay & Ackerman 2003; Tremblay *et al.* 2005). Fruits produce many seeds (over 3000 in a related species *L. rupestris*, Tremblay, unpublished) and require a mycorrhizal association for germination and survival until plants start photosynthesis. The pollinator of *L. eltoroensis* is unknown but black winged fungus gnats are known pollinators of *Lepanthes* elsewhere (Blanco & Barboza 2005). A previous study from a smaller sample size has shown that the average population sizes are small (11.6) and that the mean crowding index (a measure of distribution) was much higher (47.6) with population on average separated by 38.6 m (Tremblay 1997). The estimated lifespan is short and suggests an average of 5.2 yrs; however, it varies greatly among life stages (Tremblay 2000).

Study area

The study was carried out along an approximately 5 km section of two adjoining trails, the El Toro and Tradewind trails in the Luquillo Experimental Forest (USDA Forest Service). The trails meander in an East-West direction from Hwy 191 to Hwy 186, mainly in elfin forest habitat type, but also through palm-dominated forest in the mid-elevations. The section surveyed fluctuated between 650 m and 1050 m asl. Average annual precipitation in the elfin forest averages 4.2 m (at the nearby Pico del Este); the rainy season centres around October and the dry season in March (Wang *et al.* 2003).

At each tree where the orchid was present, the cardinal direction of the highest density of plants on the bole was noted. We also noted the range of cardinal position of the orchids on the bole. We

present the median of this range of population density of the orchid on the bole of trees, the median was calculated as the centroid of the population using the general density of orchids per area, this was estimated visually. We noted the number of individuals and life-history stage (seedlings, juveniles, and adults, Tremblay & Hutchings 2003). In almost all cases, the orchids' distribution on the bole was concentrated only over partial circumference of the tree. All individuals were counted on the trees up to approximately 3 m height; only on one tree were plants present higher than 3 m.

In general the sizes of tree boles were small and varied little with a mean and s.e. of 19.5 ± 1.63 cm. All trees were smaller than 40 cm except for one that was larger than 65 cm. A total of eleven species of trees were identified that hosted *Lepanthes eltoroensis*. In order of importance, these were: *Clusia clusioides* (Griseb.) D'Arcy, (n=16), *Prestoea acuminata* (Willd.) H.E. Moor (n= 14), *Micropholis garcinifolia* Pierre (n=12), *Ocotea spathulata* Mez (n= 6), *Tabebuia rigida* Urb. (n=6), *Cecropia peltata* L. (n=4), *Cordia borinquensis* Urb. (n=3), and a single observation for each the following trees, *Didymopanax morototoni* (Aubl.) Decne. and Planch., *Eugenia borinquensis* Britton, *Laplacea portoricensis* (Krug and Urban) Dye. All other sites with orchids were on dead trees and no identification was possible. In general, most of these trees were lacking other vascular epiphytes, in a limited number of trees bromeliads or epiphytic ferns were present (<10% of sampled sites).

Statistical analysis

Statistical tests were performed using the software JMP (ver 5.1.2) and the Circular statistics package (Jammalamadaka & SenGupta 2001) on SPlus. An introduction to circular statistics can be found in Zar (1999). Graphical representation of circular data is made using "rose diagrams" which depict the dispersion and frequencies of the measured angle. Circular distances are measured relative to 0° and consequently (in this study) the mean of the angles is relative to the magnetic north. All circular data are transformed in radians before analyses. The angular dispersion "rho = r", which is analogous to the linear scale, describes the dispersion of the data around the mean angle. Because r is a measure of concentration 1-r is a measure of dispersion ranging from lack of dispersion at 1-r = 0 to maximum dispersion at 1-r = 1. Consequently, when r = 1 all data are concentrated at the same direction (no variance) and if r = 0 this is the maximum variance and the mean angle cannot be described. The confidence intervals of the mean of the angles are calculated as provided by Zar (1999, Chapter 26). Our basic null hypotheses assume a uniform circular distribution of orchids around the bole of trees. All tests of mean direction and concentration for one or more groups follow Jammalamadaka & Sen Gupta (2001, Chapter 5) including Rao's test of uniformity and Watson's two-sample test of homogeneity. Linear and quadratic regression were used to test for a significant pattern in the relationship between DBH and population size. Population size (count data) were square root (x +3/8) transformed to normalize the data (Sokal & Rohlf 1995).

Figures were constructed with the software Oriana (Oriana ver. 2.02e; Kovach Computing Services). Shown are the Rose Diagram with frequency shown as the area of the wedge (not the radius) as recommended by Baas (2000) and Wells (2000), class width of 20°, with the mean and 95% confidence interval.

Results

Distribution of orchids on trees

Data were collected from 58 populations of *Lepanthes eltoroensis*. A total of 1007 individuals were observed with a mean of 17.3 individuals per tree. However, the population sizes were skewed with a non-normal distribution (median = 14; Shapiro Wilk test for normality $W = 0.8866$, $P < 0.0001$; Fig. 1). The number of seedlings, juveniles, and adults per tree was small (Table 1).

Table 1. Mean (standard error), median, 10th and 90th percentile of number of seedlings, juveniles and adults in 58 orchid populations of *Lepanthes eltoroensis* along the El Toro and Tradeswind trail.

	Total individuals surveyed	Mean (s.e.)	Median	10 perc-entile	90 perce-ntile
Seedlings	238	4.1 (0.76)	2	0	11
Juveniles	562	9.7 (1.16)	7	1	21
Adults	207	3.6 (0.48)	2	0	8

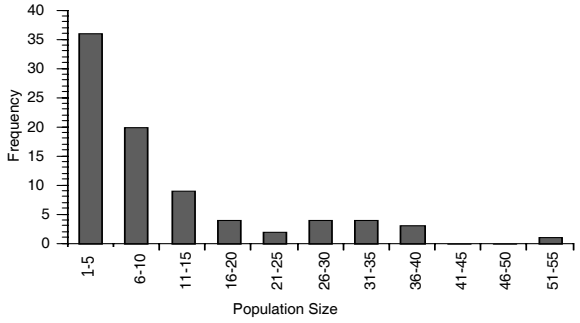

Fig. 1. Frequency distribution of number of individuals of *Lepanthes eltoroensis* on 58 trees along the Tradewinds and El Toro trails.

Population size and DBH

Most of the dbh of trees with orchids were relatively similar with a mean of 21 cm (s.e. 1.7 cm; median 18.5 cm). The size of the bole of trees does not predict the number of orchids present (linear regression on the log of DBH and square root of population size, $F_{1,54} = 0.009$, $P = 0.92$).

General results of circular distribution around the bole of trees

On individual trees, the orchids were not distributed uniformly around the bole; orchids were mainly found covering only 74º ± 6.2º (mean ± s.e.) of the bole (95% CI: 61º - 86º of the tree bole). In general, orchids were found on less than one-fourth the circumference of the bole. The general results from all population irrespective of trail or side of the trail shows an angular mean of 345º ± 31º and concentration of r = 0.353. The distribution of orchids around the bole of trees was not uniform (Rao's test of uniformity, $R = 156.10$, $P < 0.05$).

Variation among trails

We sampled 43 population along the Tradewinds Trail with a circular mean angle = 354º ± 30º, $r = 0.411$. The distribution of orchids around the bole of trees was not uniform (Rao's test of uniformity, $R = 164.9$, $P < 0.01$). There is a tendency of the orchids to prefer the northwestern side of the bole of trees on this trail (Fig. 2). We observed only 15 populations along the El Toro trail with a circular mean = 286º ± undefined, $r = 0.228$. The confidence interval is extremely wide and encompasses the whole bole. Plants around the bole of trees along the El Toro trail were not significantly different from the uniform distribution (Rao's test of uniformity, $R = 112$, $P > 0.10$). The rose diagram shows that on this trail the orchids were in the southwestern side of the trees. Comparing the distribution of orchids around the bole from the two sites suggest these are not significantly different from each other (Watson's two-sample test of homogeneity, $W^2 = 0.1346$, $P > 0.10$).

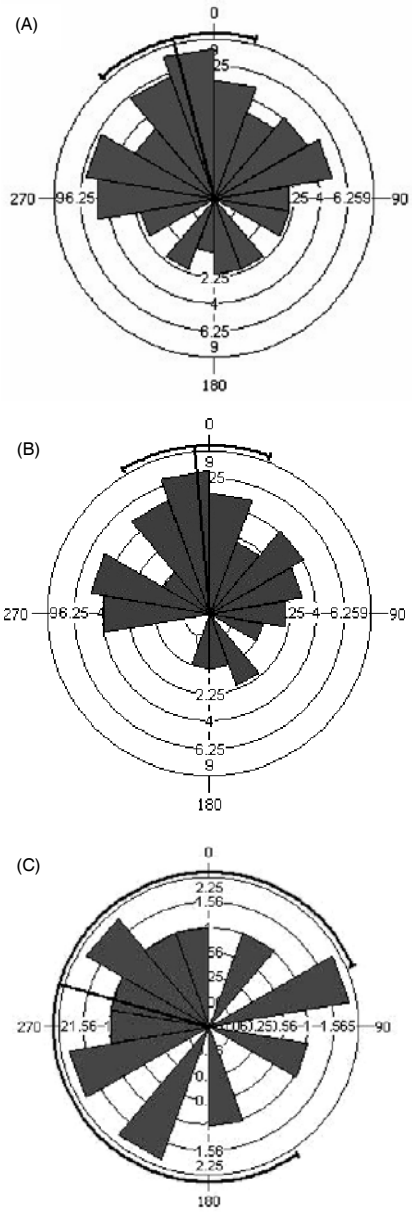

Fig. 2. Rose diagram of orchid distribution on trees along both trails, (A) all populations, (B) El Toro (n = 15), (C) Tradewinds (n = 43), on the north and south side of the trail, in the caribbean National Forest in Puerto Rico. Rose Diagrams are in equidistant groups. Longer petals represent more frequent categories. Zero degree represents magnetic north.

Discussion

The spatial distribution of the orchids was not uniform around the trunk of the trees, but preferentially occupied only a part of the tree. The populations studied showed a tendency to use the part of the trunk that faced the northwest with a mean angle of 345º ± 31º pattern of distribution was not uniform, and the orchids were sometimes concentrated in other directions. We found no evidence in the literature of the pattern of preferred cardinal position of plants on the bole of trees to compare our results, however, an extensive literature is present on the distribution of epiphytes among trees (Benavides *et al.* 2005; Benzing 1990; Flores-Palacios & Garcia-Franco 2006; Johansson 1974; Mehltreter *et al.* 2005) or on different parts of the trees (Catling *et al.* 1986) and long-term changes in vascular epiphyte assemblage (Laube & Zotz 2006). Freiberg (1996) evaluated the epiphyte distribution in a circular grid on branches, evaluating if epiphytes were positioned on the top, lateral, or lower sides of the branch, for which no differences were observed; however, circular statistics were not used to test the distribution.

It was expected that orchids would have mainly faced the trail and not the inside of the forest if light was a limiting factor. Since populations are more easily found along the trail, we hypothesized that they preferred that habitat, assuming that it was to take advantage of the additional light. However, the difficulty to sample and do transects within the forest because of the architecture of dwarf forest and the scarcity of populations and sometimes precarious landscape makes testing this hypothesis a real challenge.

The distribution of orchids mainly in the northwestern angle of the bole may reflect the constant winds coming up from the Caribbean Sea, most frequently up the ravines from a southeastern direction from the mainly easterlies and northeasterly winds attaining frequently 5.5 m s^{-1} (van der Molen 2002). It was not uncommon to observe the side of trees facing the wind had little or no moss cover while the opposite direction was covered with varying amount of moss. The pattern of moss and orchid presence has been noted in other *Lepanthes* (Tremblay *et al.* 1998) and other orchids (Kull 1998). Understanding the relationship between moss and seed germination is in its infancy (Batty *et al.* 2001, 2006; Whigham 2006). Orchid seeds require a fungi to germinate at least to the period when the seedlings are photosynthetically active (Bayman *et al.* 2002), the presence and type of moss may influence the presence of the fungi and consequently the establishment of epiphytic orchid populations.

The results show that there is a difference between the Tradewinds Trail and El Toro Trail. Most of the populations were found along the Tradewinds Trail. The difference could be because there is a difference in the floral composition along both trails. The Tradewinds Trail is mostly a Sierra Palm (*Prestoea acuminata*, Arecaceae) forest with patches of Palo Colorado (*Ternstroemia luquillensis,* Theaceae*)* trees and tall grasses while, conversely, the El Toro Trail has Palo Colorado forest with patches of Sierra Palm forest. The difference between those habitats is that the canopy of the Sierra Palm forest is more closed than the canopy of the Palo Colorado forest**.**

From this survey, we have shown that populations are small and preferentially distributed along the Tradewinds trail on trees with a DBH *circa* 21 cm with a preference for a northwestern face of the bole of trees. Other aspects of the environment require study, for example, what is the effect of light availability, quantity and quality and moss cover on establishment and persistence and consequently distribution? It is recommended that any relocation or establishment of *Lepanthes eltoroensis* populations should be mainly positioned on the northwestern face of trees to maximize survivorship.

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References

Ackerman, J.D. 1995. An orchid flora of Puerto Rico and the Virgin islands. *Memoirs of the New York Botanical Gardens.* Vol. 73. The New York Botanical Garden, Bronx, New York.

Baas, J.H. 2000. EZ-ROSE: a computer program for equal area circular histograms and statistical analysis of two-dimensional vectorial data. *Computer & Geosciences* **26**: 153-166.

Batty, A.L., D.W. Dixon, M. Brundrett & K. Sivasithamparam. 2001. Constraints to symbiotic germination of terrestrial orchid seed in a

Mediterranean bushland. *New Phytologist* **152**: 511-520.

Batty, A.L., M. Brundrett, D.W. Dixon & K. Sivasithamparam. 2006. *In situ* symbiotic seed germination and propagation of terrestrial orchid seedlings for establishment at field sites. *Australian Journal of Botany* **54**: 375-381.

Bayman, P., E.J. Gonzalez, J.J. Fumero & R. L. Tremblay. 2002. Are fungi necessary? How fungicides affect growth and survival of the orchid *Lepanthes rupestris* in the field. *Journal of Ecology* **90**: 1002-1008.

Benavides, A.M., A.J. Duque, J.F. Duivenvoorden, G.A. Vasco & R. Callejas. 2005. A first quantitative census of vascular epiphytes in rain forests of Colombian Amazonia. *Biodiversity & Conservation* **14**: 739-758.

Benítez-Joubert, R.J. & R.L. Tremblay. 2003. Efecto de remoción y relocalización de *Lepanthes eltoroensis* Stimson, despues de un Huracán. *Lankersteriana* **7**: 67-69.

Benzing, D.H. 1990. *Vascular Epiphytes*. Cambridge University Press, New York.

Blanco, M. & G. Barboza. 2005. Pseudocopulatory pollination in *Lepanthes* (Orchidaceae: Pleurothallidinae) by fungus gnats. *Annals of Botany* **95**: 763-772.

Catling, P.M., V.R. Brownell & L.P. Lefkovitch. 1986. Epiphytic orchids in a Belizean grapefruit orchid: distribution, colonization and association. *Lindleyana* **1**: 194-202.

Catling, P. M. & L.P. Lefkovitch. 1989. Associations of vascular epiphytes in a Guatemalan Cloud Forest. *Biotropica* **21**: 35-40.

Flores-Palacios, A. & J.G. Garcia-Franco. 2006. The relationship between tree size and epiphyte species richness: testing four different hypotheses. *Journal of Biogeography* **33**: 323-330.

Frangi, J.L. & A.E. Lugo. 1991. Hurricane damage to a flood plain forest in the Luquillo Mountains of Puerto Rico. *Biotropica* **23**: 324-335.

Freiberg, M. 1996. Spatial distribution of vascular epiphytes on three emergent canopy trees in French Guiana. *Biotropica* **28**: 345-355.

Jammalamadaka, S.R. & A. SenGupta. 2001. *Topics in Circular Statistics*. Series on Multivariate Analysis Vol. 5. World Scientific, Singapore.

Johansson, D. 1974. Ecology of vascular epiphytes in west Africa rain forest. *Acta Phytogeographica Suecica* **59**: 1-136.

Kull, T. 1998. Fruit-set and recruitment in populations of *Cypripedium calceolus* L. in Estonia. *Botanical Journal of the Linnean Society* **126**: 27-38.

Laube, S. & G. Zotz. 2006. Long-term changes of the vascular epiphyte assemblage on the palm *Socratea exorrhiza* in a lowland forest in Panama. *Journal of Vegetation Science* **17**: 307-314.

Mehltreter, K., A. Flores-Palacios & J.G. Garcia-Franco. 2005. Host preferences of low-trunk vascular epiphytes in a cloud forest of Veracruz, Mexico. *Journal of Tropical Ecology* **21**: 651-660.

Nieder, J., S. Engwald, M. Klawyn & W. Bathlott. 2000. Spatial distribution of vascular epiphytes (including Hemiepiphytes) in a lowland Amazonian rain forest (Surumoni Crane plot) of Southern Venezuela. *Biotropica* **32**: 385-396.

Sokal, R.R. & F.J. Rohlf. 1995. *Biometry: The Principles and Practice of Statistics in Biological Research*.3rd edn. W.H. Freeman and Company, New York.

Tremblay, R.L. 1997. Distribution and dispersion patterns of individuals in nine species of *Lepanthes* (Orchidaceae). *Biotropica* **29**: 38-45.

Tremblay, R.L. 2000. Plant longevity in four species of *Lepanthes* (Pleurothallidinae; Orchidaceae). *Lindleyana* **15**: 257-266.

Tremblay, R.L. 2008. Ecological correlates and short-term effects of relocation of a rare epiphytic herb after Hurricane Georges. *Endangered Species Research* **5**: 83-90.

Tremblay, R.L. & J.D. Ackerman. 2001. Gene flow and effective population size in *Lepanthes* (Orchidaceae): A case for genetic drift. *Biological Journal of the Linnean Society* **72**: 47-62.

Tremblay, R.L. & J.D. Ackerman. 2003. The genetic structure or orchid populations and its evolutionary importance. *Lankersteriana* **7**: 87-92.

Tremblay, R.L. & M.J. Hutchings. 2003. Population dynamics in orchid conservation: a review of analytical methods based on the rare species *Lepanthes eltoroensis*. pp. 183-204. *In:* K. Dixon, P. Cribb, S. Kell & R. Barrett (eds.) *Orchid Conservation*. Kluwer Academic Press, Perth, Australia.

Tremblay, R. L., J.D. Ackerman, J.K. Zimmerman & R. Calvo. 2005. Variation in sexual reproduction in orchids and its evolutionary consequences: A spasmodic journey to diversification. *Biological Journal of the Linnean Society* **84**: 1-54.

Tremblay, R.L., G. Pomales-Hernández & M.L Méndez-Cintrón. 2006. Flower phenology and sexual maturation: Partial protandrous behavior in three species of orchids. *Caribbean Journal of Science* **42**: 75-80.

Tremblay, R.L., J.K. Zimmerman, L. Lebrón, P. Bayman, I. Sastre, F. Axelrod & J. Alers-García. 1998. Host specificity and low reproductive success in the rare endemic Puerto Rican orchid *Lepanthes*

caritensis (Orchidaceae). *Biological Conservation* **85**: 297-304.

van der Molen, M.K. 2002. *Methodological Impacts of Land Use Change in the Maritime Tropics*. Ph.D. Thesis, Vrije Universiteit, Amsterdam, The Netherlands.

Wang, H.C., A.S. Hall, F.N. Scatena, N. Fetcher & W. Wu. 2003. Modeling the spatial and temporal variability in climate and primary productivity across the Luquillo Mountains, Puerto Rico. *Forest Ecology and Management* **179**: 69-94.

Wells, N.A. 2000. Are there better alternatives to standard rose diagrams? *Journal of Sedimentary Research* **70**: 37-46.

Whigham, D.F., J.P. O'Neill, H.N. Rasmussen, B.A. Caldwell & M.K. McCormick. 2006. Seed longevity in terrestrial orchids - Potential for persistent *in situ* seed banks. *Biological Conservation* **129**: 24-30.

Zar, J.H. 1999. *Biostatistical Analysis*. 4th edn. Prentice Hall, New Jersey**.**

Zimmerman, J.K. & I.C. Olmstead. 1992. Host utilization by vascular epiphytes in a seasonally inundated forest (tintal) in Mexico. *Biotropica* **24**: 402-407.