Chapter 39
The Population Dynamics of Epiphytic Orchids: A Review and Methodological Guide

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Summary

Epiphytic orchids represent one of the most threatened plant groups in the world. Despite the urgent need for research on their population behavior, there is a dearth of in-depth studies on the topic. Population dynamic studies using matrix analysis are a widely used tool for the management and conservation of wild plant species, but their accuracy is contingent upon high-quality field data. Obtaining field data for epiphytic orchids presents challenges far beyond those encountered for terrestrial species, due to the challenges of access and also the multidimensional space of the canopy. The diversity of orchid habitat and population structure pose additional challenges for methodological design, which are further exacerbated by the scarcity of studies documenting appropriate methods for the study of epiphytic orchids. In this review, we summarize the methodologies from existing studies and compare them. In addition, we offer new ideas and key factors to insure more accurate conservation management plans.

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1 Introduction

The study of population dynamics using matrix analysis, which estimates population growth and determines the importance of each life stage for the destiny of a population, is a widely used tool for the management and conservation of wild plant species. In recent years, matrix analysis has been used as the basis for powerful methods to model population dynamics, such as population viability analysis (PVA), which estimates the probabilities of quasi-extinction and minimal population size; the life table response analysis (LTRE), which compares the differences between lambda values of populations in different circumstances or years produced by varying vital rates; and the integration projection model, which projects population growth rates using regression models of vital rates rather than by dividing populations into stage or size classes (Silvertown et al. 1996; Menges 2000; Crone et al. 2011). The commonality shared by these methods is a strong reliance on the quality of the field-collected data used to build the models.

Among vascular plants, the Orchidaceae are one of the most threatened families in the world and constitute the largest single group covered by the Convention on International Trade in Endangered Species (CITES) and in the International Union for Conservation of Nature (IUCN 2010) Red List. Multiple causes account for the threatened status of orchids: overexploitation of wild populations, habitat loss, loss of associated mycorrhizae, specificity of substratum, and limitation of resources and pollinators (Roberts and Wilcock 2002; Batty et al. 2004).

Even though more than 100 species of epiphytic orchids are on the Red List, the population dynamics have been studied for only nine of these species. One explanatory factor for the scarcity of studies on epiphytic orchid species is the challenge of canopy access, made easily available only during the last 20 years (Lowman and Rinker 2004). Due to the urgent need for further study of orchid population dynamics, we present guidelines to inspire future research.

2 Methodology

To identify existing studies on epiphytic orchid population dynamics, we searched in multiple databases (Web of Science, Google Scholar & WorldCat) for peer-reviewed journal studies in English and Spanish. We omitted theses and dissertations. From each study, we documented the methodology used and then augmented these results using input from our own field experience to develop this guide.

3 Results and Discussion

3.1 Horizontal Distribution

Epiphytic orchids are usually distributed in clumps, encountered as patches along a transect. Usually the patch with the highest density is chosen for a survey, to attain an adequate number of individuals in each stage and thereby diminish the sampling error. Munzbergova and Ehrlen (2005) suggest marking 50 individuals for each stage to obtain good estimates. For many epiphytic orchid species, few large patches exist and/or the density of individuals in each patch is low. In those cases, we suggest labeling and measuring all individuals following the methodology used by Tremblay et al. (2006) in their analysis of small populations of lithophytic orchids.

Another important consideration is that (although it is rare to encounter phorophyte (host tree) specificity) many orchids have a preference for certain tree species. This preference may be attributed to the effect of phorophyte characteristics on the demographic processes of epiphytic orchids. For example, Frei and Dobson (1972) reported that *Quercus magnoliaefolia* Nee, *Q. cyclophylla* Liebm, and *Q. peduncularis* Nee contain substances either toxic to orchid seeds and protocorms or inhibitory to the survival of orchid seedlings. A major cause of mortality in epiphytic individuals is the instability of the substrate (flaking bark, breaking branches, or fallen trees). Consequently, phorophytes with high peeling rates are likely to result in higher rates of mortality in epiphytes than those with stable barks and the same effect is likely in soft- versus hardwood trees. Additionally, fecundity is related to the visibility and density of the plant, so phorophytes with low density of orchids and abundant foliage are likely to present lower fecundity rates. However, this is not always an important variable (e.g., Flores-Palacios and García-Franco (2003) found no relationship between orchid density and the number of flowers produced in the fruit production of the epiphytic *Rhyncholaelia glauca* Lindl). Cardelús and Clark (2010) point to a possible link between the phorophyte and the mineral nutrition of epiphytic orchid via canopy soil, potentially important due to the demographic dependence on resource availability.

Another consideration is the existence of temporal and spatial variation in the demographic process. For example, Otero et al. (2007) compared the population structures of *Psychilis monensis* in two locations and found that the site with highest seedling density also had the lowest fruit and seed production, suggesting that the best sites for pollination and seedling establishment were not the same. Schödelbauerová et al. (2010) studied population dynamics of six populations of *Lepanthes rubripetala* and found differences in lambda values among populations, concurring with the findings of Zotz and Schmidt (2006) that the variation in annual rainfall significantly affects recruitment and growth rates of smaller orchid individuals of *Aspasia principissa*. Since there is potential temporal and spatial variation, it is important to decide the length your study and also how many populations you will incorporate into the study. In this situation, more is better.

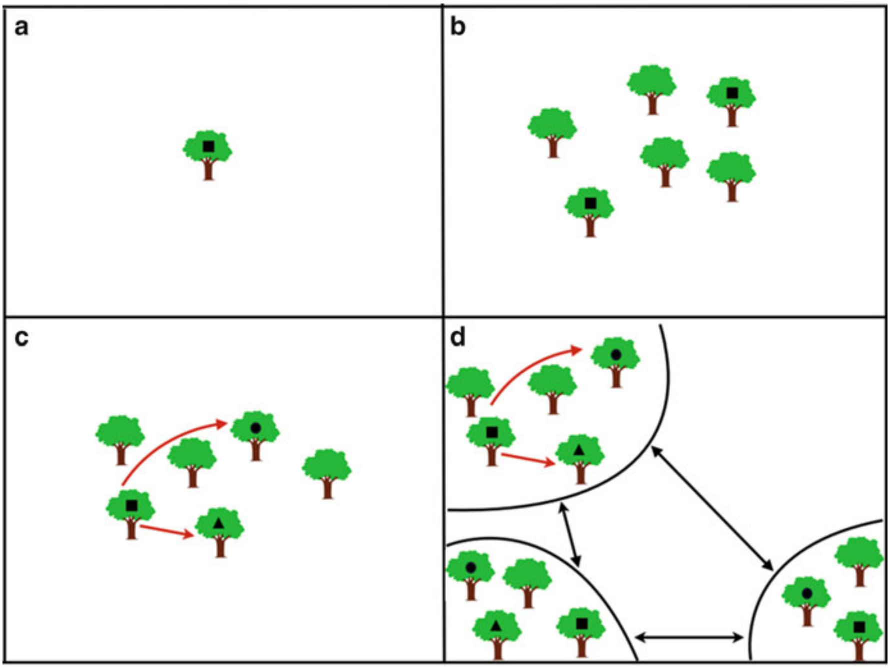

Fig. 39.1 *Squares* represent phorophytes found to have study species the first time the census was taken. *Triangles* and *circles* represent phorophytes with study species found the second and third times the census is taken, respectively. *Red arrows* represent seed dispersal within a patch and *black arrows* represent seed dispersal among patches. (**a**) A study conducted in a single phorophyte; in this case, the phorophyte is the population. (**b**) The study is conducted in a patch and all phorophytes with the study species are followed. Note the when the study was first set up, the researcher decided to only census the phorophytes that originally had the study species going back to the same phorophytes every time the census is taken. (**c**) The study is conducted in a patch using a metapopulation approach. (**d**) The study is conducted using a metapopulation approach with multiple patches

The dynamic of orchid populations can also be studied using a metapopulation approach; for groups of populations interconnected by seed dispersal, the dynamics of colonization and extinction of new patches are taken into consideration. For epiphytic orchids, this can be studied at two levels: at the patch level, where every patch is considered a population, or at the phorophyte level, where every phorophyte is considered a population (Fig. 39.1). Winkler et al. (2009) used the metapopulation approach to study the population dynamics of 3 epiphytic orchid species in Mexico. Plants growing in each phorophyte were treated as a subpopulation resulting in 1 orchid species having 5 subpopulations (5 photophytes) and 2 orchid species having 6 subpopulations each. In this study adjacent photophytes were not checked for new seedlings. Tremblay et al. (2006) also looked at the dynamics of an epiphytic/lithophytic orchid species using a metapopulation approach; however, this study looked at the occupied and unoccupied sites taking into consideration the dynamic among phorophytes (or bolders) in order to have an idea of the rate of incorporation of new phorophytes to be colonized or the loss of phorophytes in the system.

A number of questions must be answered in order for a metapopulation study for epiphytic orchids to be possible. For example, what defines a patch? What is the minimum number of individuals needed for a patch or a tree to be considered a population? How many species of phorophytes are necessary to conduct an accurate evaluation of the metapopulation process?

In order to apply the metapopulation approach at the patch level rather than at the phorophyte level, the kind of ecosystem being studied is an important consideration. When working in a forest where most of the canopy is interconnected, we suggest setting up a metapopulation study at the patch level. Alternately, when working in an ecosystem where phorophytes are separated by more than 5 m, we recommend setting up the metapopulation study at the phorophyte level.

3.2 Vertical Distribution

In some ecosystems, the microclimatic variation from the top to the bottom of the trees restricts the distribution of certain epiphytic species. Johanson (1974) identifies five vertical zones and subsequently researchers have fused or adapted these zones to account for the specificities of the ecosystem being studied. In these cases, it is important to delimit one part of the tree as a population for labeling. This step is not necessary in ecosystems where microclimatic differentiation is weak or when studying generalist species; in these cases, individuals throughout the entire tree must be labeled in order to capture the full range of variation. Labeling individuals throughout all areas of the tree is essential due to the potential effects of location on germination and seedling survival, as well as mortality due to dislodgement; different parts of the tree are more susceptible to lose bark and broken branches.

When working with tall trees, we recommend using climbing equipment and conducting the census and labeling from bottom to top; in smaller trees, a ladder can provide better accessibility. General safety precautions apply to all canopy work: avoid trees with wasp or bee hives, assess the weight bearing capacity of each species being climbed, and avoid diseased or dead trees.

3.3 Individual Labeling

The best surveying practice for labeling individuals is to work from bottom to top, following a branch. Individuals are frequently dislodged after the initial survey but can be identified easily in subsequent visits by interpolating from the anterior and posterior labels. The proper choice of materials greatly increases success in the difficult environment of the canopy. Aluminum or plastic labels offer the best resistance to weathering and the use of bright colors, such as red and blue, facilitates the surveying process, just as the use of green, brown, or black labels will hinder efforts to locate tags. An additional option is to use brightly colored wire to fix labels, in the event that brightly colored labels are not available.

3.4 How to Measure

In order to evaluate the demography of the population, it is necessary to follow the destiny of the individuals of the sample population. Many epiphytic orchid species have the ability to produce new independent individuals with the same genetic identity originated from the vegetative meristem (Harper 1977). You can follow the dynamic in two different ways (Harper and White 1974): (1) at the genet level, where the generation of each new ramet is considered a growth of the parent genet (Harper 1977; De Kroon and van Groenendael 1997), and/or (2) at the ramet level, where the generation of each new ramet is considered a new individual (Piquot et al. 1998).

When monitoring at the ramet level, the natality and mortality rate of the ramet only affects the size of the individual plant. On the other hand, the natality and mortality rate of genet has a direct influence on the effective size of the entire population having strong influence in the ecology and evolution of the species (Cook 1983).

When monitoring at the ramet level, each pseudobulb is considered a single individual. When monitoring at the genet level, each group of ramets is considered a genet. It can be discerned between genets since the connection among pseudobulbs can be easily broken or hidden under moss or other epiphytic plants, making the same genet appear as two different individuals. It is also possible for the genet to grow until it reaches a neighboring genet making it hard to tell individuals apart.

Once the individual unit being monitored is defined, estimators can be identified to measure the growth, fecundity, and survival of the individuals. For epiphytic orchids, the pseudobulbs are storage organs for water and minerals, and some also have photosynthetic functions (Yew and Hew 2000), so they are very important for the survival, growth, and fecundity of the individuals. In Table 39.1, we present the estimators that have been used in epiphytic orchid demographic studies. Most studies use the number and/or size of the pseudobulb, but in species that have no pseudobulbs, the number of leaves may be used. There are no studies for leafless species, like *Harrisella porrecta*. In this case, the lack of leaves and pseudobulbs leaves the option of measuring the individual stems.

Measuring plant survival can be straight forward; however, in some cases, even when the pseudobulbs look dead in 1 year, surprisingly a live plant can be found the next year the population is visited. If an apparently dead plant is found, wait at least 2 years to confirm it. In terms of fecundity, it is believed that epiphytes have a seed bank (Benzing 1990). Consequently, fecundity is estimated based on the number of protocorms produced by an adult individual, rather than on the number of seeds

Table 39.1 Structures and measures used in epiphytic orchid population dynamics studies

Species	Stages based on	Growth structure measured	Fecundity	
Aspasia principissa[a]	Length	Pseudobulb		F=# of seedling/# of ind. in reproductive categories
Erycina crista-galli[b]	Height and number and presence of rs	Pseudobulb	Fr	F=# of seedling/# of ind. in reproductive categories
Jacquiniella leucomelana[c]	Length of the longest	Ramet	Fr, Fl	F=# of seedling/# of reproductive plants
J. teretifoli[c]	Length of the longest	Ramet	Fr, Fl	F=# of seedling/# of reproductive plants
Guarianthe aurantiaca	Height and number, and presence of rs	Pseudobulb	Fr	F=# of seedling/# of ind. in reproductive categories
Lepanthes caritensis[d]	Height, and presence of rs	n/a	Fr, Fl	F=# of seedling/# of reproductive plants
L. eltoroensis[e]	Presence, and presence of rs	Lepanthiform sheet	Pollinaria, Fr	F=# of seedling/# of reproductive plants
L. rubripetal[f]	Presence, and presence of rs	Lepanthiform sheet		n.a.
Lycaste aromatica[c]	Volume and number, and presence of rs	Pseudobulb	Fr, Fl	F=# of seedling/# of reproductive plants

Fl flowers, *Fr* fruit, *rs* reproductive structures
[a]Zozt and Schmidt 2006
[b]Mondragón et al. 2007
[c]Winkler et al. 2009
[d]Tremblay 1997
[e]Schödelbauerová et al. 2010
[f]Tremblay and Hutchings 2003

being produced. This avoids creating a delay of a year in the matrix (Caswell 2001). It can be very hard to find protocorms because they are so small and can be hidden in cracks on the phorophyte stem or inside moss mats. It is easier to find seedlings because they are bigger, which is why most of the orchid studies evaluate fecundity based on number of seedlings found. When seedlings become visible, they are very delicate and can be easily detached, so it is important not to put a label on the seedling itself. Instead, it is more effective to attach a pin or tag on the stem or branch near the seedling. It is important to be consistent in the distance and orientation of the pin and to maintain detailed notes, to facilitate finding plants on subsequent visits for data collection. Also, you may find a large number of seedlings growing together; in this case, make an imaginary square with four pins surrounding the group of seedlings and count and measure them. Again, take good notes. If you have different adult categories, you will need to count the number of fruits that each adult produced, in order to give the proportion of seedlings that each adult category produced in function of the proportion of total fruit produced by that category.

Finally, when visiting the field site to take a new census, bring the measures from the previous time. This can be extremely helpful since you may need help locating a plant with a lost tag or accessing dead individuals.

4 Conclusion

Here we addressed key knowledge gaps in methods for epiphytic orchid research, which hinders research on population behavior critical to conservation management efforts of epiphytic orchid species. There is an urgent need of new research that can incorporate a metapopulation approach that takes into consideration spacial and temporal variations.

We suggest that it is necessary that more studies of epiphytic orchid species be conducted, specifically:

- The demography of species with different morphological characteristics (e.g., deciduous species, species without leaves, species without pseudobulbs)
- The demography of species in different types of ecosystems (e.g., temperate forest, dry forest, costal dune)
- The comparison of the population dynamics growing in different types of phorophytes
- Incorporation of the metapopulation concept at the patch level

References

Batty AL, Dixon KW, Brundrett MC, Sivasithamparam K (2004) Orchid conservation and mycorrhizal associations. In: Sivasithamparam K, Dixon KW, Barrest RL (eds) Microorganism in plant conservation and biodiversity. Springer, Netherlands

Benzing DH (1990) Vascular epiphytes. Cambridge University Press, New York

Cardelús CL, Mack MC (2010) The nutrient status of epiphytes and their host tree along an elevational gradient in Costa Rica. Plant Ecol 207:25–37

Caswell H (2001) Matrix population models: construction, analysis and interpretation. Sinauer, Sunderland

Cook RE (1983) Clonal plant populations: A knowledge of clonal structure can affect the interpretation of data in a broad range of ecological and evolutionary studies. American Scientist 71: 244–253

Crone EE, Menges ES, Ellis MM, Bell T, Bierzychudek P, Ehrlen J, Kaye TN, Knight TM, Lesica P, Morris WF, Oostermeijer G, Quintana-Ascencio PF, Stanley A, Ticktin T, Valverde T, William JL (2011) How do plant ecologist use matrix population models? Ecol Lett 14:1–8

Flores-Palacios A, García-Franco JG (2003) Effects of floral display and plant abundance on fruit production of *Ryncholaelia glauca* (Orchidaceae). Rev Biol Trop 51:71–78

Frei SJK, Dodson CH (1972) The chemical effect of certain bark substrates on the germination and early growth of epiphytic orchid. Bull Torrey Bot Club 99:301–307

Harper JL (1977) Population biology of plants. Blackburn Press, England. 922 pp

Harper J, White J (1974) The demography of plants. Annual Review of Ecology and Systematics 5:419–463

IUCN (2010) IUCN red list of threatened species. Version 2010.2. www.iucnredlist.org

Johanson D (1974) Ecology of vascular epiphytes in West African rain forest. Uppsala University

Kroon HD, Groenendael JV (1997) The ecology and evolution of clonal plants. Backhuys Publishers

Lowman MD, Rinker HB (2004) Forest canopies. Academic, San Diego

Menges E (2000) Population viability analyses in plants: challenges and opportunities. Trends Ecol Evol 15:51–56

Mondragón D, Maldonado C, Aguilar-Santelises R (2007) Life history and demography of a twig epiphyte: a case study of *Erycina crista–galli* (Orchidaceae). Selbyana 28:137–144

Munzbergova Z, Ehrlen J (2005) How best to collect demographic data for population viability analysis models. J Appl Ecol 42:1115–1120

Otero JT, Aragón S, Ackerman JD (2007) Site variation in spatial aggregation and phorophyte preference in Psychilis monensis (Orchidaceae). Biotropica 39:227–231

Piquot Y, Petit D, Valero M, Cuguen J, de Laguerie P, Vernet P (1998) Variation in sexual and asexual reproduction among young and old populations of the perennial macrophyte Sparganium erectum. Oikos 139–148

Roberts DL, Wilcock CC (2002) Fragmentation of tropical rainforests and its effect on orchid survival. In: Nair H, Arditti J (eds) Proceedings of the 17th world orchid conference “Sustaining Orchids for the Future”, Natural History Publications, Borneo

Schödelbauerová I, Tremblay R, Kindlmann P (2010) Prediction vs. reality: can a PVA model predict population persistence 13 year later. Biodivers Conserv 19:637–650

Silvertown J, Franco M, Menges E (1996) Interpretation of elasticity matrices as an aid to the management of the plant population for conservation. Conserv Biol 10:591–596

Tremblay RL (1997) *Lepanthes caritensis*, an endangered orchid: no sex, no future? Selbyana 18:160–166

Tremblay RL, Hutching MJ (2003) Population dynamics in orchid conservation: a review of analytical methods, based on the rare species *Lepanthes eltoroensis*. In: Dixon KW, Kell SP, Barrett RL, Cribb PJ (eds) Orchid conservation. Natural History Publications (Borneo), Kota Kinabalu

Tremblay RL, Meléndez-Ackerman E, Kapan D (2006) Do epiphytic orchids behave as metapopulations? Evidence from colonization, extinction rates and asynchronous population dynamics. Biol Conserv 129:70–81

Winkler M, Hüber K, Hiez P (2009) Population dynamics of epiphytic orchid in a metapopulation context. Ann Bot 104:995–1004

Yew CK, Hew CS (2000) Orchid pseudobulbs – ‘false’ bulbs with a genuine importance in orchid growth and survival. Sci Hortic 83:165–172

Zotz G, Schmidt G (2006) Population decline in the epiphytic orchid *Aspasia principissa*. Biol Conserv 129:82–90