

PART OF A HIGHLIGHT ON ORCHID BIOLOGY

## When stable-stage equilibrium is unlikely: integrating transient population dynamics improves asymptotic methods

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- **Background and Aims** Evaluation of population projection matrices (PPMs) that are focused on asymptotically based properties of populations is a commonly used approach to evaluate projected dynamics of managed populations. Recently, a set of tools for evaluating the properties of transient dynamics has been expanded to evaluate PPMs and to consider the dynamics of populations prior to attaining the stable-stage distribution, a state that may never be achieved in disturbed or otherwise ephemeral habitats or persistently small populations. This study re-evaluates data for a tropical orchid and examines the value of including such analyses in an integrative approach.
- **Methods** Six small populations of *Lepanthes rubripetala* were used as a model system and the R software package popdemo was used to produce estimates of the indices for the asymptotic growth rate ( $\lambda$ ), sensitivities, reactivity, first-time step attenuation, maximum amplification, maximum attenuation, maximal inertia and maximal attenuation. The response in  $\lambda$  to perturbations of demographic parameters using transfer functions and multiple perturbations on growth, stasis and fecundity were also determined. The results were compared with previously published asymptotic indices.
- **Key Results** It was found that combining asymptotic and transient dynamics expands the understanding of possible population changes. Comparison of the predicted density from reactivity and first-time step attenuation with the observed change in population size in two orchid populations showed that the observed density was within the predicted range. However, transfer function analysis suggests that the traditional approach of measuring perturbation of growth rates and persistence (inertia) may be misleading and is likely to result in erroneous management decisions.
- **Conclusions** Based on the results, an integrative approach is recommended using traditional PPMs (asymptotic processes) with an evaluation of the diversity of dynamics that may arise when populations are not at a stable-stage distribution (transient processes). This method is preferable for designing rapid and efficient interventions after disturbances, and for developing strategies to establish new populations.

**Key words:** Transient population dynamics, stable-stage equilibrium,  $\lambda$ , reactivity, first-time step attenuation, maximum amplification, maximum attenuation, maximum inertia, transfer function, population projection matrices, PPM, orchids, *Lepanthes rubripetala*, Orchidaceae, Puerto Rico.

### INTRODUCTION

Biologists, conservation managers and decision makers with interest in the trajectories of population dynamics need tools that are easy to use and interpret, apply across a wide range of taxa and give results that predict future population sizes with the highest possible confidence. The preferred approach has been to use asymptotically based population projection matrices (PPMs) as a set of models that have tractable outcomes, including calculations of asymptotic growth rates, population stable distributions, elasticities, sensitivities, damping ratios etc. (Caswell, 2001). Stochastic PPM models are a modification of these approaches and explore the likely changes in population dynamics over time as a consequence of demographic, spatial and environmental variation (Tuljapurkar, 1997; Fieberg and Ellner, 2001; Lande *et al.*, 2003).

Although these models are commonly employed in the ecological and conservation literature, little attention has been given to the accuracy and effectiveness of PPM models (Kephart and Paladino, 1997; Bierzychudek, 1999; Coulson *et al.*, 2001; Lindborg and Erhén, 2002; Van Mantgem and Stephenson, 2005; Schödelbauerová *et al.*, 2010; Jäkäläniemi *et al.*, 2013). So what is the predictive power of population projection analyses? In a recent review of the population dynamics of 82 populations of 20 species, Crone *et al.* (2013) found that in more than half of the studies using PPMs the actual population sizes over a period of time were either above or below the projected confidence intervals, suggesting weaknesses in the methods, the data or both.

An alternative, novel and infrequently considered approach for characterizing population dynamics over time is to use transient dynamics, which are fluctuations describing how much

populations vary as a consequence of stochastic events prior to reaching asymptotic growth and achieving a stable-stage distribution. Originally part of the robust control theory of engineering, several attempts have been made to include transfer functions in the population ecology and conservation management toolbox (Rebarber and Townley, 1995; Hodgson and Townley, 2004). Caswell (2007) developed an approach to analyse transient sensitivities and elasticities using matrix calculus, but more recently Stott *et al.* (2010a, 2011, 2012a, b) offered a series of set of functions, which are available in R (popdemo package; R Project for Statistical Computing, 2013), to investigate short-term time series as a consequence of ecologically, environmentally and anthropologically induced perturbations. The traditional way to assess the effects of perturbations on demographic parameters using sensitivity analysis relies on eigenvectors and gives a linear approximation that could be misleading for non-linear responses. This was addressed by Stott *et al.* (2012b), who calculated sensitivities without using eigenvectors through a derivative process based on transfer functions (McCarthy *et al.*, 2008). One of the advantages of the transfer function is that it only needs to specify the magnitude of the perturbation of a demographic parameter to describe the non-linear changes in that parameter. Furthermore, transient dynamics may be more appropriate for conservation because it addresses outcomes that are more likely to occur within the time frame of a management project (Ezard *et al.*, 2010).

To complement asymptotic and transient analysis, we use transfer functions to perform an analysis of the population dynamics of a Neotropical orchid by assessing the non-linear changes in asymptotic growth produced by changes in transition parameters. We re-analyse the data of Schödelbauerová *et al.* (2010) on *Lepanthes rubripetala* using transient dynamics and transfer function tools and compare the observed dynamics and likely persistence of the population with the stochastic simulations from Schödelbauerová *et al.* (2010). We hypothesize that for many small populations, using *only* the traditional PPM models, based on stable-stage distribution and asymptotic growth rate, is likely to be either misleading or give a different perspective on the likely population dynamics under study.

## METHODS

### Data collection

Our model species was *Lepanthes rubripetala*, Orchidaceae, which is endemic to the Caribbean island of Puerto Rico and is a member of a large genus (>1100 species; Govaerts *et al.*, 2014) renowned for its narrow endemism (Crain and Tremblay, 2014). All but one of 120 species in the Caribbean are single-island endemics (Ackerman, 2012; Luer, 2014). *Lepanthes rubripetala* is a small epiphytic or epipetric species restricted to shady, montane wet habitats. The caespitose plants grow sympodially, with each slender stem bearing a single leaf. The terminal, fasciculate racemes are adpressed to the underside of the leaf and produce flowers in succession, usually one at a time, throughout the year. The flowers are 3–4 mm long. Fruit and seed production is pollinator-dependent and flowers are protandrous (Tremblay *et al.*, 2006), and infrequently pollinated; pollination is probably the result of fungus gnat pseudocopulation (Blanco and Barbosa, 2005; Tremblay and Ackerman, 2001).

The small scattered populations of this species make a good model system because plant size and lifespan are manageable for demographic work. Furthermore, relatively few studies have been conducted on the demographic dynamics of tropical plants, especially herbaceous ones.

Our data are the same as those of Schödelbauerová *et al.* (2010), who selected six populations distributed along three streams: Río Grande and Quebrada Grande along the western slopes of the Luquillo Mountains in the El Yunque National Forest; and Río Patillas at Charco Azul in the Carite State Forest. Three hundred and eighty-one individuals of *L. rubripetala* were marked and observed monthly from June 1994 to January 1996. Population sizes at the first survey were 84, 17, 49, 86, 101 and 44. At each observation period, the numbers of leaves, flowers and fruits were counted and individuals from all populations were classified as seedlings, juveniles, non-reproductive adults and reproductive adults. These categories are defined as follows (Tremblay and Hutchings, 2003; Rivera-Gómez *et al.*, 2006): seedlings are small plants without lepanthiform sheaths on any shoot; juveniles are individuals with at least one lepanthiform sheath on the stem and lack evidence of past or current inflorescences; non-reproductive adults have dried inflorescences from a previous flowering event, but they are not currently flowering; reproductive adults have active inflorescences that have buds, flowers and/or fruits (the theoretical life cycle of *L. rubripetala* is illustrated in Fig. 1).

### Population dynamics analysis and comparisons

The traditional approach of asymptotic analysis of PPMs focuses on long-term population dynamics to predict population trajectories. Stable-stage distributions (the predicted population structure when asymptotic growth rate is attained) and sensitivities (a measure evaluating the effect of absolute change of a parameter on growth rate) are calculated, which are density-independent and time-invariant indices (Caswell, 2001). Transient-based evaluation of PPMs is also time-invariant, but by varying the starting demographic distribution as a consequence of demographic stochasticity, whether of biotic, abiotic or anthropogenic origin, an initial stage distribution is obtained that diverges from the stable-stage distribution. This difference leads initially to either a short-term increase in population size/density (*amplifications*) or a short-term decrease (*attenuation*). If no other perturbations or disturbances are present (e.g. hurricanes, flash floods, landslides, biotic invasions), then the transient dynamics models are expected to settle to the stable-stage distribution. The time it takes to reach the stable stage is the transient period (Stott *et al.*, 2011). Transient population dynamics are usually not evaluated in most published PPM articles; however, indices such as the damping ratio (Caswell, 2001), Keyfitz's delta (Keyfitz, 1968) and Cohen's cumulative distance metric (Cohen, 1979) are sometimes considered surrogates for considering the transient dynamics of populations, but they have limitations (Stott *et al.*, 2011).

We calculated, using the package popdemo in R (R Project for Statistical Computing, 2013), the following indices of transient dynamics as described by Stott *et al.* (2011), and includes the expected lower and upper limits of change in the first-time step: *reactivity* (maximum population growth in a single time

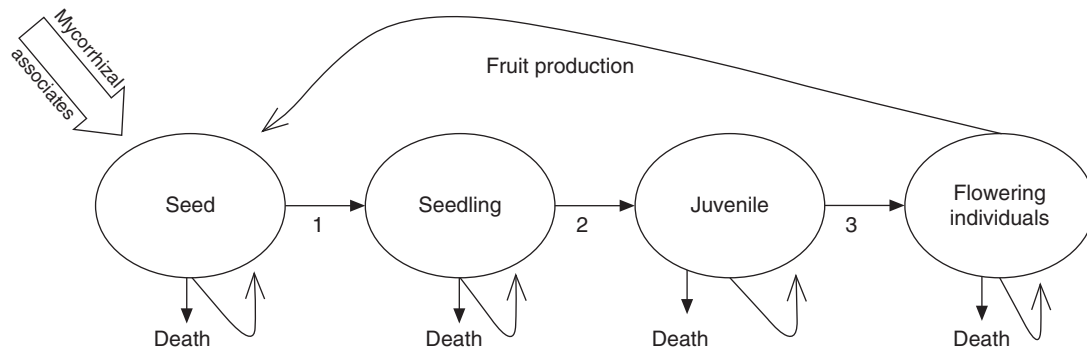


FIG. 1. The theoretical life cycle of *Lepanthes rubripetala*. For successful germination, seeds must be colonized by mycorrhizal fungi to form protocorms, which subsequently grow into juveniles, non-reproductive adults or reproductive adults. Once adulthood is achieved, the plant remains an adult; however, adults move readily among reproductive and non-reproductive phases within a year.

step relative to stable-stage growth), *first-time attenuation* (minimum population growth in a single time step relative to stable-stage growth), *maximal amplification* (the largest possible future population size relative to a stable growth rate and same initial population size) and *maximal attenuation* (the smallest possible future population size relative to a stable growth rate and the same initial population size). We also calculated two other indices: *amplified inertia* (the largest long-term population size relative to a population with stable growth rate and the same initial density) and *attenuated inertia* (the smallest long-term population size relative to a population with stable growth rate and the same initial density). In other words, populations that have not achieved a stable-stage distribution are likely to achieve long-term population density at a fixed ratio below or above the expected stable-stage distribution (Stott *et al.*, 2012b).

Natural perturbations affect the demographic parameters of a population to different degrees (Hodgson and Townley, 2004; Hodgson *et al.*, 2006). Consequently, we present the response of asymptotic growth rate ( $\lambda$ ) to perturbations of demographic parameters using a transfer function and multiple perturbations of growth, stasis and fecundity.

Moreover, we investigate the expected effect of changes in parameter estimates on  $\lambda$  using a non-linear function (Stott *et al.*, 2012b). Transfer functions are commonly used in the analysis of linear, time-invariant systems such as single-input, single-output filters. They allow one to calculate the relationship between  $\lambda$  and the intensity of perturbation ( $\delta$ ). We only need to define the position of the vital rate perturbed through two vectors,  $\mathbf{e}$  and  $\mathbf{d}$ , the intensity of the perturbation, with one scalar,  $\delta$ , to obtain the new asymptotic growth rate as a consequence of the perturbed vital rate. The exact relationship between perturbation and growth rate was given by Hodgson and Townley (2004) as:  $\delta^{-1} = \mathbf{e}^T (\lambda \mathbf{I} - \mathbf{A})^{-1} \mathbf{d}$ .  $\mathbf{A}$  is a generic way to indicate the matrix population of the species we are working with, in our case all of six populations of *L. rubripetala* have  $(4 \times 4)$  dimension.  $\mathbf{I}$  is the identity matrix with the same dimension of  $\mathbf{A}$ . Inertia in the context of transient dynamics measures how much larger or smaller a population changes compared with an equivalent population at stable-stage distribution (Stott *et al.*, 2012b). Non-stable populations show different growth patterns compared with populations at stable distribution, ultimately resulting in long-term population densities above or below those predicted if the population was at a stable

distribution (Stott *et al.*, 2012b). This long-term persistence is termed *inertia*. *Inertia* is calculated as the ratio between the long-term population densities at non-equilibrium above an equivalent stable population (Koons *et al.*, 2007; Stott *et al.*, 2012b). Consequently, populations with *inertia* values  $>1$  become and remain larger whereas those with *inertia*  $<1$  are smaller and remain smaller. Transfer function plots of inertia for the whole life cycle for the six populations of *L. rubripetala* were evaluated for the upper and lower bounds and the case-specific inertia for the current population structure.

Non-linear sensitivities were calculated (*tfmatrix* function in the popdemo package) and compared with the original linear approach. We tested the assumptions of reducibility and ergodicity for matrices using the tests as described in Stott *et al.* (2010b), and all were met.

To evaluate how transient dynamics mirror real population growth rates, we compared the change in population size across 17 time periods with the extremes of population growth and reduction (*reactivity* and *first-time attenuation*), which evaluated the likely range of change in the first time step with a time lag of 1 with  $n$  equal to the number of observed individuals in the time period in each of the observed stages.

The PPMs are available in [Supplementary Data S1](#).

## RESULTS

### *Transient dynamics*

The transient indices suggest that the range of amplitude of predicted population densities over the first time interval is substantial. Populations in which the structure is dominated by seedlings are expected to have large reductions in population size (density), resulting in a *first-time attenuation* ranging from 0.84 to 0.57, suggesting that in one time period populations could be reduced to 57 % of the expected stable-stage distribution. When populations are dominated by reproductive adults, the expected population densities increase due to *reactivity* in the first time step, suggesting that populations could increase by 11–18 % (Fig. 2, Table 1).

The same two initial conditions, only seedlings or only reproductive adults, could have long-term effects on population density. The long-term expected reduction, *maximal attenuation*, could be dramatic, with density reductions ranging from 13 to 73 % in the transient period (Fig. 2, Table 1). On the other

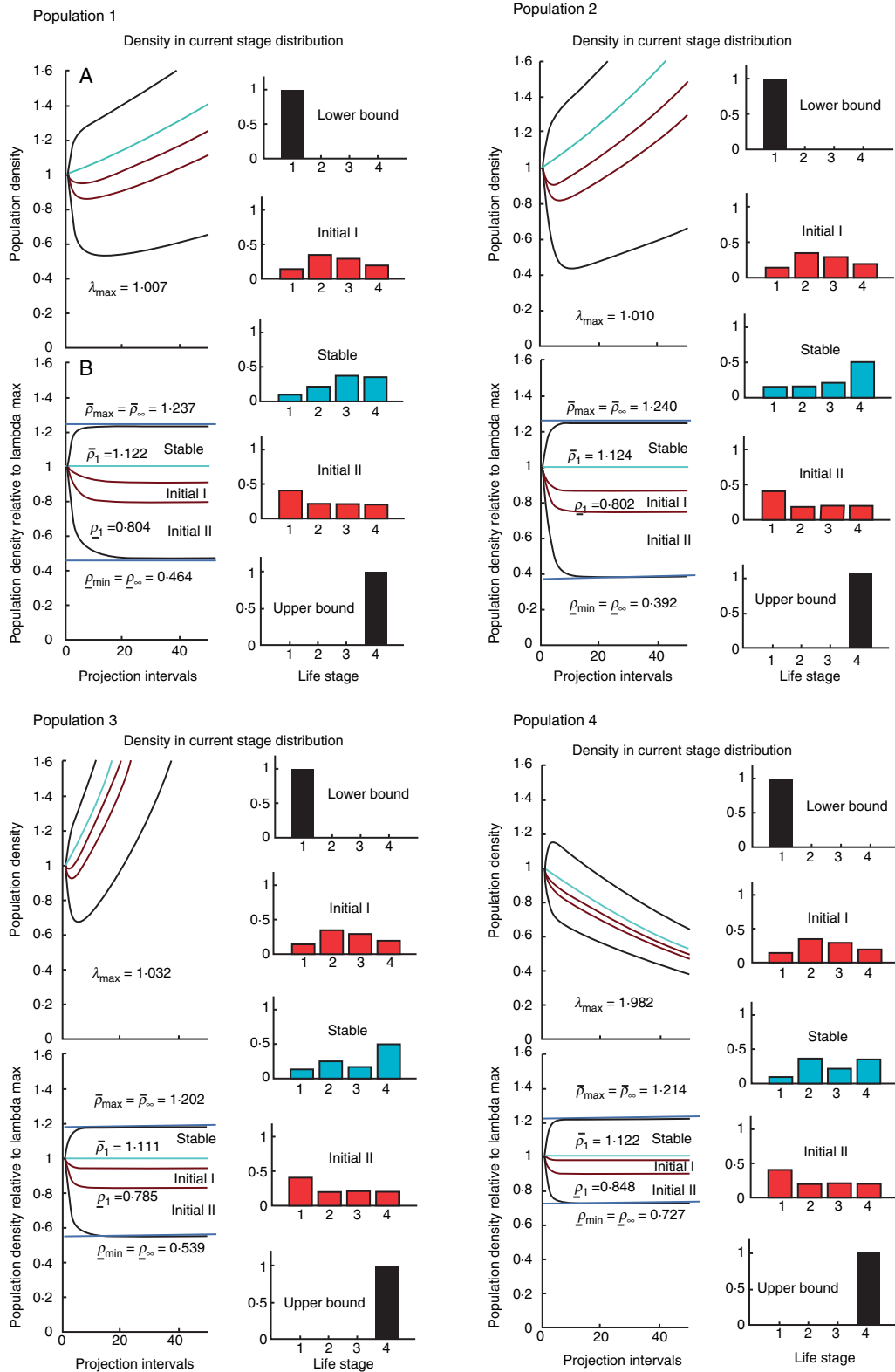


FIG. 2. (A) Absolute population dynamics, including transient and asymptotic influences, for the six populations of *Lepanthes rubripetala*. (B) Standardized transient dynamics, excluding the influence of asymptotic growth for *L. rubripetala*. All demographic distributions are scaled to an initial population density sum 1. The transient bounds for *L. rubripetala* are superimposed on the graph. We simulated five initial conditions. The two black bar plots at top and bottom correspond to having all individuals in the smallest and largest class, respectively. The two red bar plots correspond to distributions between the above distributions, and the blue bar plot corresponds to a stable demographic distribution. Bias distribution of individuals among stages: bias1 = [1 0 0 0]; bias2 = [0.15 0.35 0.30 0.20]; bias3 = stable-stage distribution (varies among matrices); bias4 = [0.4 0.2 0.2 0.2]; bias5 = [0 0 0 1].

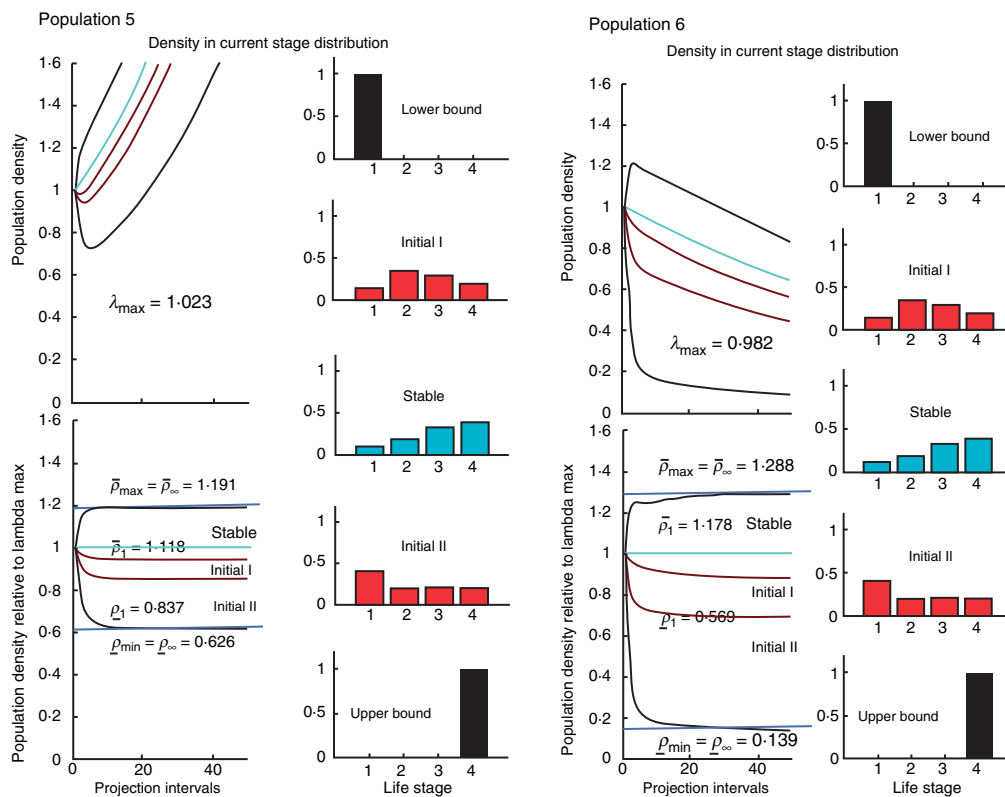


FIG. 2. Continued

TABLE 1. Predicted stochastic asymptotic growth ( $\lambda$ ) of six *Lepanthes rubripetala* populations deterministic and stochastic  $\lambda$  (the 95 % confidence interval of the s.e. of the stochastic  $\lambda$ ) and transient dynamics: reactivity, first-time step attenuation, maximum amplification, maximum attenuation and upper and lower bound inertia (see Methods section for explanation of indices, stochastic lambdas from Schödelbauerová et al., 2010)

Population	Deterministic lambda/stochastic lambda (s.e.)	Reactivity	First-time step attenuation	Maximum amplification	Maximum attenuation	Amplitude inertia (upper bound)	Attenuation inertia (lower bound)
1	1.007/1.0072 (1.0070–1.0074)	1.122	0.805	1.237	0.464	1.237	0.464
2	1.010/1.0161 (1.0159–1.0163)	1.125	0.802	1.240	0.393	1.240	0.393
3	1.028/1.011 (1.0108–1.0113)	1.112	0.786	1.202	0.539	1.202	0.539
4	0.982/0.9824 (0.9782–0.9801)	1.123	0.848	1.214	0.728	1.214	0.728
5	1.024/1.0233 (1.0230–1.0236)	1.118	0.837	1.191	0.627	1.191	0.627
6	0.987/1.0075 (1.0072–1.0079)	1.180	0.567	1.301	0.133	1.301	0.133

hand, the expected pattern of *maximal amplification* is no more than 19–30 %, a much smaller proportional change compared with the *maximal attenuation*. The *amplified inertia* also ranges from 19 to 30 %, whereas the expected range of *attenuated inertia* is 13–73 % (Fig. 2, Table 1).

### Transfer functions

The general pattern for the non-linear sensitivities, i.e. *transfer function* analysis on  $\lambda$  (Fig. 3, population 1; and Supplementary Data S2, populations 2–6), shows that parameters below the diagonal, which indicate the probability of growth from one growth class to another in one time interval, are more or less linear, whereas the diagonal (the probability of individuals staying in the same stage) are clearly non-linear.

Thus, change in stasis could be misleading solely by using the traditional method of calculating sensitivities as a likely predictor of the impact of absolute changes of the parameter on  $\lambda$  (Supplementary Data S4).

The non-linear response of inertia to perturbation shows a more complex pattern of relationships compared with the effect on  $\lambda$  (Fig. 4; Supplementary Data S3). The effects of perturbation on inertia were evaluated for the upper and lower bounds and case-specific results for each population are shown in Appendix 3. As an example of the complex dynamics, the non-reproductive adults remaining in this stage show a double-hump inertia response. The density of the population would be expected to increase by 24 % as result of a small reduction in this stasis parameter in population 1, whereas no such density change is expected in population 2. However, in both populations a density increase is expected. Another equally variable

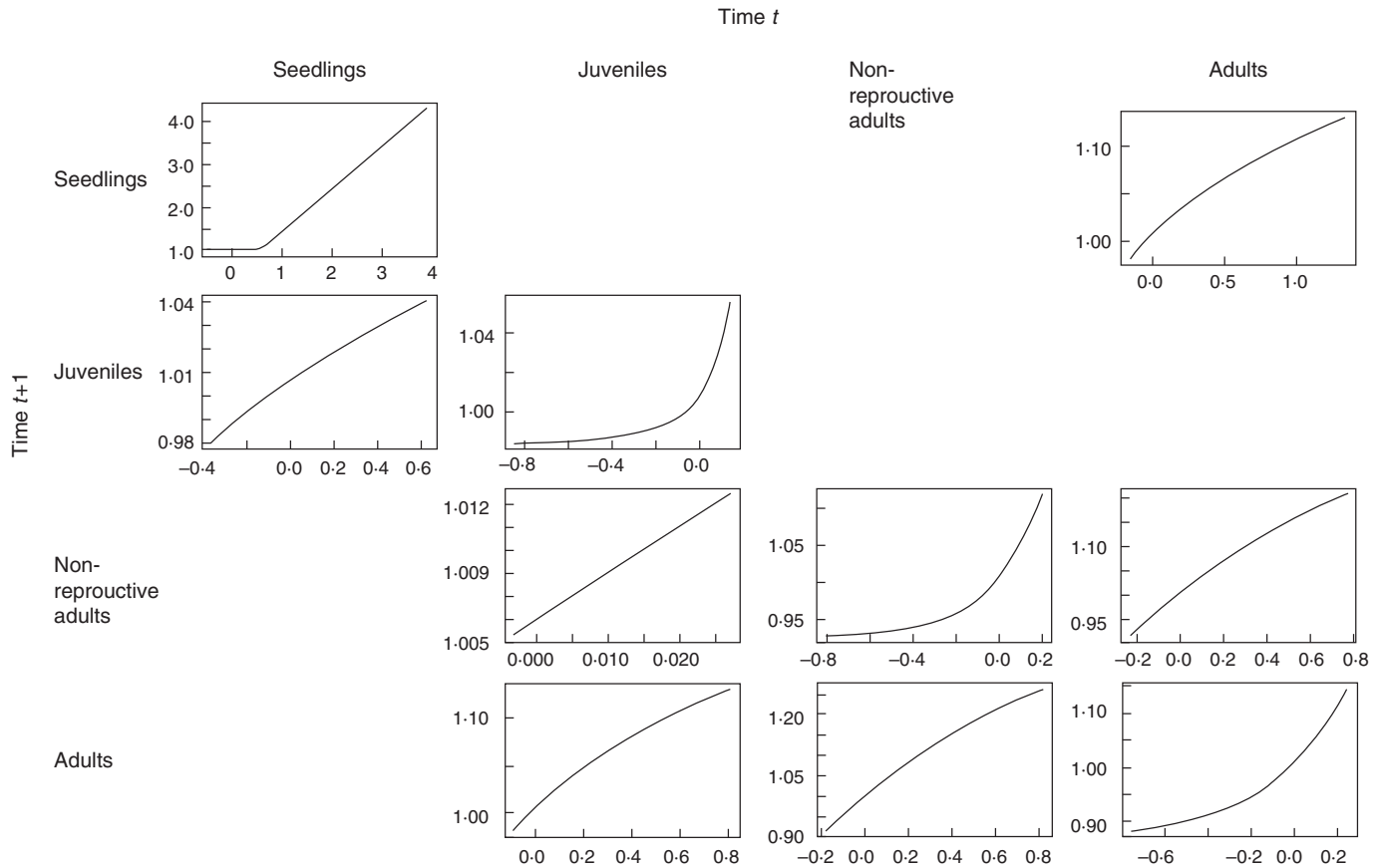


Fig. 3. Transfer functions between transition parameters and the resulting changes in asymptotic growth rate,  $\lambda$ , for population 1 of *L. rubripetala* (see [Supplementary Data S2](#) for other populations). Each graph represents the effect of change in  $\lambda$  as a function of change in the parameter while holding the other parameters constant. A graph is produced only if a parameter is present in the matrix for the specific transition. In general, we see that most changes in the transition of growth (below the diagonal) have close to a linear effect on  $\lambda$  (but none is linear), but in stasis (the diagonal) the effect of changes in parameters is clearly non-linear.

response in inertia is observed in the transition from the non-reproductive to the reproductive stage for the case-specific population structure, where the response is a decreasing function (populations 1, 2 and 5), an increasing function (population 3) or a complex response (populations 4 and 6). These complex variable patterns of inertia are observed in many of the transitions.

#### Observed versus expected population density changes

Observed population densities of *L. rubripetala* were similar to the predicted *first-time attenuation* and *reactivity* for the complete 17 time periods in the two populations evaluated (populations 1 and 5) (Fig. 5). The number of individuals was too low in the other populations for a reasonable comparison.

## DISCUSSION

Schödelbauerová *et al.* (2010) reported results of PPM analysis using an asymptotic approach and noted that if population growth rates are consistent and the expected stable population distributions are reached, four populations of *L. rubripetala* (populations 1, 2, 3 and 5) are expected to grow, whereas two are expected to decline (populations 4 and 6). The asymptotic

growth rate (non-stochastic) ranged from 0.987 to 1.029 (Fig. 2, Table 1). With the same data set but integrating transient dynamics and transfer function tools, we found that the road to stable-stage distribution is non-linear and the starting population structure at the beginning influences population densities.

The expected transient dynamics of the surveyed populations varied among populations of *L. rubripetala* and population density could be expected to change readily. The transients among populations varied in their predicted projection in the different indices. One of the conspicuous patterns is that populations are much less likely to have large increases in density (*reactivity* and *maximum amplification*) compared with reduction (*first-step attenuation* and *maximum attenuation*). For species that are rarely if ever found in large numbers (Tremblay, 1997), this suggests that populations could be reduced or even disappear much more readily than they can increase in size, thus not only influencing population persistence (Morris and Doak, 2002) but also leading to the possibility of reduction in the effective population size (Tremblay and Ackerman, 2001).

The asymptotic behaviour of all six populations of *L. rubripetala* showed growth rates near to 1, five of them slightly above 1, and one slightly below 1, which means that a population of *L. rubripetala* as a whole tends to show long-term

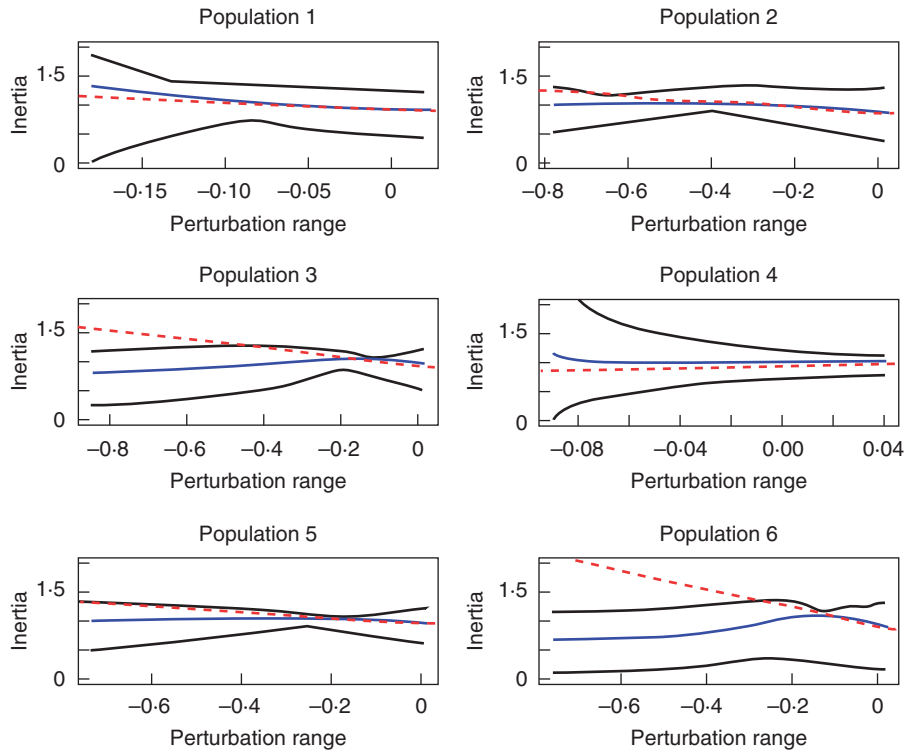


FIG. 4. Transfer function plots of population inertia for the elements that have the maximum sensitivity value of the whole life cycle for each of the six populations of *Lepanthes rubripetala*. On each plot, the two black lines represent the upper and lower bounds of population inertia, respectively; the blue line represents the transfer function of the current population structure for each population; and the dashed red line represents sensitivity at zero perturbation.

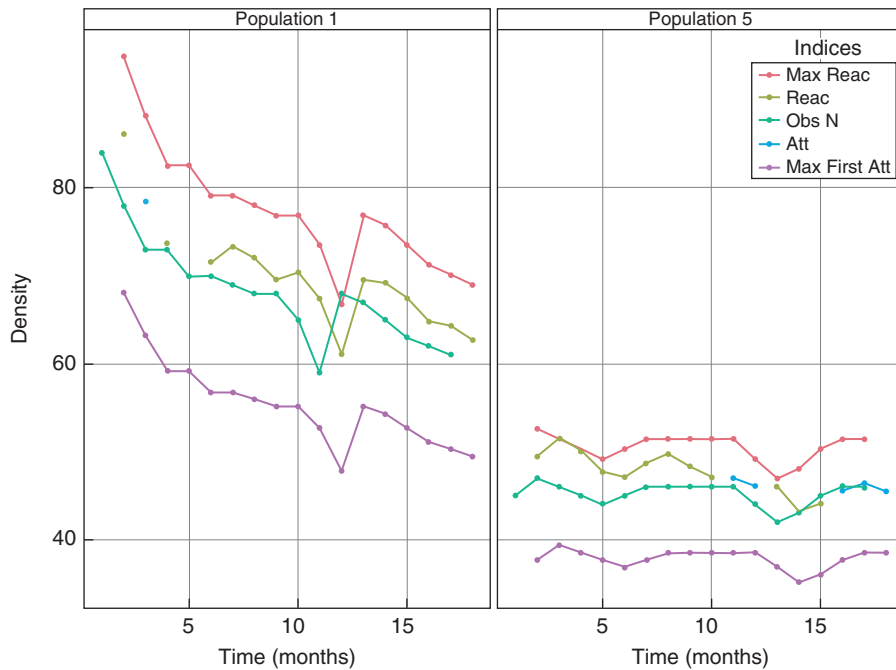


FIG. 5. Observed population density, *first-time attenuation* and *reactivity* for the 17 time periods for populations 1 and 5. First-time attenuation and reactivity are the expected changes in density for a given time period as determined by the change in population demographic structure. Maximal reactivity (Max Reac) and first-time step (Max Att) attenuation are the results of biasing the population towards reproductive adults or seedlings, respectively, attenuation (Att) and reactivity (Reac) are the expected decrease or increase in density as a function of the observed sample size at time  $t-1$ , and the observed line (Obs N) is the density of the surveyed population at time  $t$ .

stationary behaviour. However, due to uncertainty associated with the process of demographic stochasticity and the fact that parameters are estimated from small sample sizes, it is risky to make a statement regarding the 'true' state of the transition parameters. Therefore, parameter estimates should always include confidence intervals and some measure of uncertainty in the PPMs. Furthermore, parameters for each population could be better estimated using a Bayesian approach by including information from all populations (Tremblay and McCarthy, 2014). Demographic stochasticity (important for small population sizes) and environmental stochasticity (flash floods, hurricanes, tree falls) can result in a loss of many individuals and result in variation in parameter estimates and ultimately variation in the population growth rate (Morris and Doak, 2002). The likely effect of demographic stochasticity was explicitly modelled by Schödelbauerová *et al.* (2010), who showed that in all populations of this orchid the density of future populations could be drastically reduced, and most simulation outcomes included the probability of populations going extinct.

A comparison of transient dynamics and population growth outcomes after 13 years (from Schödelbauerová *et al.*, 2010) shows that population 4, which went extinct, had the lowest transient dynamic range among all surveyed populations. This population went extinct after a flash flood (December 1995) that resulted in the removal of all but one large individual from the population due to the force of the water. The remaining plants perished in the following months. In populations that are continuously perturbed by the environment, as are these orchids, evaluation of the growth pattern by asymptotic processes may not reflect the possible change in population size even if the species is long-lived, because attaining a stable-stage distribution may take much longer than the frequency of disturbance. Disturbance is probably a common process in epiphytic and lithophytic species, so realization of a stable-stage distribution may be an uncommon phenomenon. Thus, limiting the application of PPMs to the evaluation of asymptotic population dynamics may not appropriately reflect extinction risks.

The observed number of individuals was consistently similar to the predicted number of individuals (Fig. 3). In the absence of immigration and migrations or disturbance, population dynamics should be similar. Noting densities outside the predicted bounds should be considered a rare event. For example, strongly biased dynamics would be expected for founder populations comprising only seedlings or relocated populations of a few reproductive adults.

The absolute density of the population may not follow the attenuation predicted by the transient dynamics, as in Fig. 3, if  $\lambda > 1$ ; thus, population density could be relatively lower at  $t + 1$  compared with an equivalent population at stable-stage distribution, but absolutely higher than at  $t$ . Biologically, the PPM may not necessarily represent adequately the recruitment process in *Lepanthes*. Fruits can have many seeds (~6000), and the recruitment process is variable and unpredictable and unlikely to follow a simple pattern, whereas stochastic demographic recruitment will influence density by overestimating attenuation. In this PPM model recruitment distribution may be unrealistic, because the recruitment is likely to have a Poisson distribution with low mean probability but an extremely flat and wide probability distribution. However, we are still

ignorant of recruitment processes across time and space in natural populations of orchids and how best to model these in a realistic fashion (Ackerman *et al.*, 1996; Murren and Ellison, 1998; Raventos *et al.*, 2011; Jacquemyn *et al.*, 2012).

Transfer function analyses were consistent among all six populations. The slope represents the likely rates of change of  $\lambda$  as a function of change in the parameter estimates. Consequently, if small changes (increase or decrease) in survivorship/stasis are applied to juveniles, non-reproductive adults and reproductive adults staying in the same stage would have the largest effect on growth rates compared with equivalent changes in parameters with smaller slopes. Environmental fluctuations will result in changes in the parameters of stasis and transitions, so that population growth rates will probably change as well. Although a shift in environmental conditions will cause a proportional change in the parameters, it does not necessarily result in proportional change in growth rate, nor is the proportional response likely to be linear. Thus, predicting the influence of growth rate as a function of linear responses (sensitivities) is likely to be misleading. Consequently, we suggest that transfer functions be used to evaluate non-linear responses to changes in parameters instead of the traditional measures of sensitivities. In addition, Hodgson and Townley (2004) showed a similar pattern in that the curvature of response seems to be more pronounced in the stasis parameters than in the growth parameters in the desert tortoise.

Inertia, the persistence of the increase or decrease in population density as a consequence of perturbations and not being at a stable-stage equilibrium is extremely variable and varies among populations. This extreme variation in the pattern of inertia among populations would make it difficult to predict the response to an equal perturbation in an unevaluated sister population. Nevertheless, some patterns are evident: populations dominated by the later life stages result in positive inertia, whereas populations dominated by early life stages are likely to have persistent small population densities. Consequently, founder events are likely to be either disastrous or result in a long period at low densities.

For populations that are frequently perturbed because of flash floods as a consequence of tropical storms and hurricanes, the concept of stable-stage/age distribution and the parameters that are dependent on this index may be unrealistic. Transient indices may be more amenable to the needs of wildlife managers and conservation biologists because they describe the range of possible outcomes from diverse starting points in population size and structure. Pielke *et al.* (2003) pointed out that many locations in the tropics had at least a 10 % chance of experiencing a hurricane annually. In these areas the occurrence of hurricanes shows high inter-annual variability and large multidecade changes.

An additional difficulty is in the use of elasticities and sensitivities, which occurs when categorizing continuous variables to make the model fit a discrete model of stage structure, as in the PPM approach. Biases may emerge if different categorical cutoff points that are selected influence the relative importance of growth stage and survival rates (Enright *et al.*, 1995). When the matrices are constructed from continuous variables, integral projection models (IPMs) should be the preferred way to evaluate PPMs (Easterling *et al.*, 2000; Ellner and Rees, 2006;



Metcalf *et al.*, 2013), but these are limited as they do not yet incorporate transient analysis.

As a general pattern, transient dynamics are strongly dependent on initial conditions (i.e. a population composed only of seedlings will have trajectories different from those of a population composed only of adults; Stott *et al.*, 2010a). Fortunately, the first years of a reintroduction programme or new founding populations can be evaluated to determine the range of likely density changes in subsequent years. Such analyses could provide better choices for determining the initial population structure that could maximize long-term persistence.

*In situ* species conservation requires knowledge not only of ecological variables that influence life history stages, but also of how they enhance the likelihood of species/population persistence. A drawback of asymptotic growth rates and related indices is that they do not readily include estimates of the transient dynamics and variation in growth rates and stage distributions prior to attaining the asymptotic growth rate and the expected stable-stage distribution. Thus, an integrative approach could elucidate alternative scenarios of population dynamics for the conservation management of species. We recommend unifying the study of PPMs using the traditional asymptotic analysis with an evaluation of the diversity of dynamics that may arise when populations are not at a stable-stage distribution.

#### SUPPLEMENTARY DATA

Supplementary Data are available online at [www.aob.oxfordjournals.org](http://www.aob.oxfordjournals.org) and consist of the following. Data S1: population matrices of the six populations of *L. rubripetala* and calculation of transition parameters. Data S2: sensitivities of non-linear relationship between changes (permutations) in transition parameters and the resulting change in the asymptotic growth rate, lambda, for the six populations of *L. rubripetala*. Data S3: transfer functions plots of inertia for the whole life cycle for the six populations of *L. rubripetala*. Data S4: sensitivity matrices as 3-D surface plots for the six populations of *L. rubripetala*.

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#### LITERATURE CITED

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