

Fungal symbionts maintain a rare plant population but demographic advantage drives the dominance of a common host

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Summary

1. A potential driver of species abundance that remains understudied is the interaction between host species and their microbial symbionts. Beneficial symbionts could promote the dominance of common host species by increasing their population growth rates more than they do for rare species, and symbiont benefits could be important for maintaining rare species in communities. Alternatively, intrinsic differences in demography, independent of interactions with symbionts, could be the main driver of species' relative abundances.

2. Here, we used demographic modelling with 5 years of data from experimental host populations to compare how symbiotic fungal endophytes, which are vertically transmitted from parent plant to offspring, influenced the population dynamics of one pair of co-occurring, congeneric rare versus common host grasses (genus *Poa*).

3. The common plant species achieved higher population growth than the rare species. Endophyte symbiosis increased the geometric population growth rate (λ) of rare and common species by 18% and 32%, respectively, but only the rare species was predicted to decline ($\lambda < 1$) in the absence of the endophyte, demonstrating that symbiosis was essential to maintain this species in the community.

4. Endophyte symbiosis differentially affected the demographic transitions of the two hosts, increasing survival and growth for the common host, *Poa sylvestris*, and increasing survival but decreasing the probability of flowering for the rare host, *Poa alsodes*. The total contribution of the endophyte effects on host demographic rates to the overall difference in population growth between host species was small compared to the plants' intrinsic differences in demography. However, low rates of vertical transmission in *P. sylvestris* lessened its advantage in intrinsic demography over *P. alsodes* and thus decreased the projected difference in population growth between host plants.

5. Synthesis. Our results highlight the importance of plant–symbiont interactions in the persistence of a rare plant population, as well as the utility of demographic models in teasing apart the relative importance of plant demographic rates versus host–symbiont interactions on the regional abundance of rare and common host plant species.

Key-words: commonness and rarity, demography, *Epichloë*, fungal endophyte, integral projection model, mutualism, plant population and community dynamics, symbiosis, vertical transmission

Introduction

The majority of hypotheses to explain variation in species abundance focus on differences in species traits, such as reproductive investment, dispersal and resource requirements (Kunin & Gaston 1997). One potential driver of variation in abundance that remains understudied is the assemblage of

microbial symbionts that grow in host tissues. Symbiosis with microbes is a ubiquitous phenomenon in nature (Douglas 1994), but has historically been overlooked as a driver of host species abundance and distribution. This topic has received increasing attention during the past decade as tools for investigating microbiomes have developed, and keystone symbioses (e.g., corals – dinoflagellates) have responded to global change (Hoegh-Guldberg 1999). In terrestrial systems, results indicate that plant–microbe symbioses can have strong influences on individual host plant fitness (Reynolds *et al.* 2003;

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Bever, Platt & Morton 2012), which suggests that microbial symbiosis can be a driver of species-level variation in abundance within an ecosystem. For example, effects of plant–soil microbial interactions have been shown to be more detrimental to rare than common species in an old field system (Klironomos 2002). Alternatively, instead of being more beneficial for common species, mutualistic symbioses could allow for the persistence of a rare species in the face of superior competitors (Phillips *et al.* 2014). The effects of symbioses on host species abundance should be stronger in symbiotic interactions that are strongly coupled, such as in vertically transmitted symbioses, since vertical transmission is expected to select for host–symbiont mutualism. However, the role of heritable symbiosis as a driver of variation in species abundance remains poorly understood.

In vertically transmitted (from parent to progeny) symbioses, in which the benefits and costs of cooperation ultimately feedback to affect both parties, the fitness of host and symbiont is tightly coupled (Sachs *et al.* 2004). In such situations, not only could symbionts differentially affect the population dynamics of rare and common hosts, but the population dynamics of hosts can also feedback to determine the population dynamics of the symbiont (Yule, Miller & Rudgers 2013). Due to positive fitness feedbacks, beneficial symbionts are expected to reach fixation in host populations (e.g. Ewald 1987). However, imperfect vertical transmission, whereby some fraction of offspring from symbiotic parents are symbiont free, can prevent symbiont fixation (Gundel *et al.* 2008). Therefore, both variation in the vertical transmission rate and in the benefit of symbiosis to host population growth can determine natural frequencies of symbiosis (Gundel, Rudgers & Ghersa 2011; Miller & Rudgers 2014). However, the relative importance of these two pathways to the fitness, frequency and abundance of symbionts and hosts is poorly understood for natural populations.

Quantifying the effect of symbiosis on population dynamics can be challenging. The interaction outcome between symbionts and hosts can vary in magnitude and sign throughout the ontogeny of the host (Bronstein 1994; Rudgers *et al.* 2010). Therefore, the effects of a symbiont at any one stage of host development may not accurately indicate its net effects over the host's life time (Palmer *et al.* 2010). Ontogenetic shifts also provide a potential mechanism by which rare and common host species can differ in the dynamics of host–symbiont interactions. Comparisons between rare and common species often show differences in life history strategies (Kunin & Gaston 1997), which could interact with ontogenetic shifts in host–symbiont interactions throughout host life cycles to differentially affect rare and common species. Thus, characterizing the ecological dynamics of symbioses (and other species interactions) across host ontogeny is essential to determining how these interactions manifest at the population level (Palmer *et al.* 2010; Rudgers *et al.* 2010, 2012). In order to evaluate the contribution of symbiosis to variation in host species abundance and population growth, it is necessary to separate the differential outcomes of symbiosis from difference in intrinsic (symbi-

ont-free) host demography, a goal we address here for the first time.

Demographic models are a useful but under-utilized tool for evaluating the population-level consequences of species interactions and comparing the consequences of different life history strategies (Crone *et al.* 2011). Compared to investigations at the individual level, which evaluate individual performance at particular life stages (e.g. seed production, biomass, survival), few studies have taken a demographic modelling approach to comparing rare and common species (but see Byers & Meagher 1997; Münzbergová 2005; Esparza-Olguín, Valverde & Mandujano 2005; Münzbergová 2013). Here, we used size-structured demographic models to identify the demographic rates that contribute most to population growth and that are most affected by symbiosis for a pair of rare and common species. We considered symbiotic and symbiont-free members of host populations by using integral projection models (Ellner & Rees 2006) to describe transitions between host sizes (via demography) and symbiont status (via imperfect transmission). For the first time, we specifically address the relative contributions of differences in symbiosis outcome, vertical transmission and intrinsic demography to the differences in population growth between host taxa. We also explore the dynamic from the symbiont's perspective by investigating how differences between hosts in their interactions with symbionts influence the persistence of symbionts in host populations.

In this study, we focused on a pair of co-occurring rare and common grass hosts (*Poa alsodes* and *Poa sylvestris*, Poaceae) that associate with vertically transmitted fungal endosymbionts in the genus *Epichloë*. Grass–endophyte interactions are generally assumed to be beneficial to the grass host (Clay 1990). However, the majority of evidence comes from research in agriculturally important species (Cheplick & Faeth 2009), and few studies have investigated native grass–endophyte interactions, particularly at the population level (but see Rudgers *et al.* 2012; Yule, Miller & Rudgers 2013). Recent work has shown that vertically transmitted fungal endophyte symbioses can exhibit ontogenetic shifts in interaction outcome (Rudgers *et al.* 2012; Yule, Miller & Rudgers 2013), highlighting the need for experimental studies that take a population demographic approach. To our knowledge, this study is the first to experimentally test the effects of endophyte symbiosis on grass hosts at the population level in a comparative context. The results of this study not only expand previous knowledge on the population-level consequences of grass–endophyte symbioses, but situate symbioses generally into the broader framework of studies on rarity versus commonness (e.g. Gaston 2011).

Specifically, we asked the following questions: (1) How does endophyte symbiosis affect host demographic rates and ultimately influence rates of host population growth? (2) Do the effects of endophyte symbiosis on host demographic rates and population growth differ between rare and common species? We predicted that endophyte symbiosis could promote the dominance of the common host species by increasing its population growth rate more than for the rare species. Alternatively,

the dominance of the common species could be driven more by intrinsic demographic advantages than by the benefits of endophyte symbiosis. We also examined dynamics from the perspective of the symbiont and asked, (3) Do populations of rare and common host species differ in the expected level of symbiont persistence? Finally, throughout our investigation of questions 2 and 3, we asked (4) What is the role of imperfect vertical transmission in host population growth and symbiont persistence?

Materials and methods

STUDY SPECIES

Poa alsodes (grove bluegrass) and *P. sylvestris* (woodland bluegrass) are caespitose, woodland perennials of similar stature (30–70 cm tall), which flower and fruit from early May to mid-June. Phylogenetically, the two species are grouped with five other North American species in *Poa* sect. *Sylvestres* (Barkworth *et al.* 2007), an early diverging lineage of *Poa* (Gillespie, Soreng & Smith 2005). In Indiana, both species are reported from mesic woods dominated by beech-sugar maple (Deam 1929). *Poa alsodes* is state-listed as rare in Indiana (with few records for the state) and has endangered status in Illinois, which represents the western edge of its range (USDA and NRCS 2013). Despite extensive surveys, we have found only one population of *P. alsodes* in southern Indiana with two other county records reported; however, historical records indicate multiple populations along the shore of Lake Michigan in the northern part of the state (Deam 1929). *Poa sylvestris* reaches as far west as South Dakota and eastern Texas, and has been recorded in most counties in Indiana (USDA and NRCS 2013). *Poa alsodes* hosts an unnamed species of *Epichloë* (formerly genus *Neotyphodium*) (Schardl *et al.* 2007; Shymanovich *et al.* 2013). *Poa sylvestris* is known to host *Epichloë typhina* subsp. *poae* (Moon *et al.* 2004; Leuchtman *et al.* 2014), but some host grasses harbour more than one *Epichloë* species (Schardl 2010), and we have not genotyped the endophytes studied here. Both endophytes appear to be exclusively vertically transmitted through host seeds; we have not observed stromata (the sexual structures for horizontal transmission) nor have stromata been reported elsewhere (Clay & Leuchtman 1989).

STUDY SITES

Seeds of both species were collected from natural populations at the Indiana University Research and Teaching Preserve at Lilly Dickey Woods, Nashville, Indiana, USA (39°14'54"N, -86°13'05"W). In 2 years, we randomly sampled ~30 plants each from populations of *P. alsodes* (24 May 2006, 26 Jun 2007) and *P. sylvestris* (9 June 2006, 7 June 2007). Endophyte frequency in the *P. alsodes* populations (92–100% endophyte-symbiotic) was higher than that in the *P. sylvestris* population (69–86% endophyte-symbiotic).

EXPERIMENTAL METHODS

Half of the collected seeds were heat-treated (7–10 days at 60 °C in convection oven) to remove endophytes. Once the lemma and palea were removed, heat-treated and control seeds were placed in a cone of filter paper and surface-sterilized by rinsing once in 1% Tween-80, three times in 1% sodium hypochlorite, then three times in sterile H₂O. Seeds were then cold-stratified on 2% water agar at 4 °C for

4 weeks (Rudgers *et al.* 2012). We transplanted emergent seedlings into 115 mL pots (Conetainers; Stuewe and Sons, Canby, OR, USA) filled with ProMix BX potting soil (Premier Horticulture, Quakertown, PA, USA) and watered daily. Plants were split to produce equally sized ramets planted into separate pots. To evaluate endophyte status, we applied aniline blue-lactic acid stain to thin sections of the inner leaf sheath (Bacon & White 1994). Stained tissue was examined under a compound brightfield microscope at 200–400 \times . Only individuals (ramets) for which the endophyte was present or effectively eliminated were planted into the field experiment.

In the field experiment, we planted two cohorts (September 2007 and April 2008) of field plots consisting of 100% endophyte-symbiotic plants (E^+) or 100% endophyte-free plants (E^- , endophyte-removal treatment). Plots were located at the Lilly Dickey Woods Preserve near, but not overlapping with, sites where both species occurred naturally (39°14.19'–39°14.23', -86°13.03' to 86°13.12', elevation 289–294 m). Within a plot, each of the 20 plants had the same endophyte status but represented a unique genotype; thus, all plots had the same level of initial genotypic diversity. Plants were added to the natural matrix of vegetation with minimal disturbance. For each cohort, we planted five replicate E^+ and five replicate E^- populations, excepting that the 2008 cohort of *P. alsodes* had only four replicates of each treatment. Plots were positioned ~5 m apart to minimize seed dispersal between plots. Endophyte treatment was randomly assigned to each plot.

We collected demographic data annually during peak seed production before seeds had dispersed during late May/early June of 2008–2012. For each individual plant, we recorded survival, the number of tillers and the number of flowering culms. We estimated seed production for each plant by counting the number of spikelets per culm for three randomly chosen culms plant⁻¹; then, we multiplied the number of culms \times the number of spikelets culm⁻¹ \times mean number of seeds spikelet⁻¹ (*P. alsodes* mean seeds per spikelet = 2.06 \pm 0.027 SE, $N = 501$ spikelets, t -test for endophyte effect $P = 0.116$, *P. sylvestris* mean seeds per spikelet = 1.86 \pm 0.022 SE, $N = 558$ spikelets, t -test for endophyte effect $P = 0.179$). Each year, we also marked all new recruits per plot using a uniquely labelled aluminium tag secured with an aluminium nail. We tracked growth and reproduction for recruits that survived beyond the first year. We calculated the probability of seedling establishment per plot as the number of recruited seedlings divided by the estimated total number of seeds produced by all parent plants in the plot in the previous year, adjusted for any seeds removed for vertical transmission trials (see next section).

To assess endophyte vertical transmission rates, we removed a subset of seeds from the originally planted individuals still surviving during May 2009, ~30 seeds from each plot. For *Poa alsodes*, we examined 179 seeds from E^+ plots and 193 seeds from E^- plots. For *P. sylvestris*, we examined 331 seeds from E^+ plots and 289 seeds from E^- plots. Batches of ~10 seeds per plot were surface-sterilized as above and placed in 2% water agar on sterile, 10-cm Petri plates for 6 weeks of cold stratification at 4 °C and then transferred to the glasshouse. To assess vertical transmission rates, we examined seedlings for endophyte presence using rose bengal stain following Belanger (1996). Vertical transmission was analysed using a binomial generalized linear mixed model with the fixed effect of endophyte treatment and the random effect of plot nested within endophyte treatment.

INTEGRAL PROJECTION MODEL

To obtain asymptotic population growth rates (λ) for each species with or without endophyte symbiosis, field data were used to parameterize

a size-structured integral projection model (IPM). IPMs provide a framework to predict how vital rates measured at the level of individuals scale up to affect population dynamics, including λ , the geometric rate of population growth. In the context of our study, IPMs allow us to evaluate the population-level consequences of the demographic effects of endophyte symbiosis, and the contrast between host species allows us to decompose the difference in population growth into ‘intrinsic’ demographic differences versus differences in interactions with symbionts. Here, we provide a brief overview of the IPM structure. Further information is provided by several recent papers addressing the construction and applications of IPMs (Coulson 2012; Metcalf et al. 2013; Merow et al. 2014; Rees, Childs & Ellner 2014).

The IPM predicts the change in size structure of a population, $n(y)$, over size domain Ω , from time t to $t + 1$ as:

$$n(y)_{t+1} = \int_{\Omega} [p(y,x) + f(y,x)]n(x)dx. \tag{eqn 1}$$

Size-dependent survival and growth are represented by:

$$p(y,x) = s(x)g(y,x), \tag{eqn 2}$$

$s(x)$ is the probability of survival for individuals of size x , and $g(y,x)$ is the probability of a surviving individual growing from size x to size y . Reproduction, $f(y,x)$, representing the production of y -sized plants from x -sized parents, is given by:

$$f(y,x) = r(x)f_n(x)pE d(y), \tag{eqn 3}$$

$r(x)$ is the size-dependent probability of flowering and $f_n(x)$ the seed production of plants that flowered. These two functions are multiplied by pE , the probability of seedling establishment (size-independent), and $d(y)$, the probability distribution of seedling size. These demographic functions together constitute an IPM kernel which describes all possible transitions between sizes in a single year. Construction and analysis of the IPM were conducted in R 3.0.0 (R Core Team 2013).

MODEL PARAMETERIZATION

Functions describing the size-dependent growth, survival and reproduction of each species were fit using generalized linear models with the appropriate error distribution. Data across all years (2008–2012) were pooled into single interannual (t to $t + 1$) transitions. We used the natural logarithm of tiller number (range: 1–125 and 1–93 for *Poa sylvestris* and *P. alsodes*, respectively) as the dependent variable, size (x, y). While tiller number is itself a discrete variable, here we use its natural log as a proxy for continuous variation in biomass following Yule, Miller & Rudgers 2013. Seed production $f_n(x)$ was fitted with a Gaussian linear model using the natural log number of seeds as a response and exponentiated to predict seed counts.

For each demographic function, endophyte symbiosis could affect vital rate functions through the slope of the vital rate (y-axis) against size (x-axis) (size-dependent effects), the intercept of this relationship (size-independent effects), both, or neither. Thus, for each demographic function, we fit data to four possible models: no endophyte effects (size-dependent only), endophyte effect on intercept, endophyte effect on slope, and endophyte effect on both slope and intercept (Table 1). We used Akaike’s information criterion (AIC) to evaluate model fit, and AIC weights to discriminate between models. For all fitted demographic functions, no single model AIC weight was > 0.9. Therefore, we used AIC weights to weight coefficients for model averaging across the four models (Table 1, Burnham & Anderson 2002). Observed rates of seedling establishment, pE , were

logit-transformed and analysed using a repeated measures generalized linear mixed model with year and endophyte status as fixed effects and plot nested within endophyte status as a random effect (PROC GLIMMIX, SAS v. 9.3, Cary, NC, USA). Seedling establishment varied widely between years for both species. Therefore, we modelled λ against the observed range of probabilities of establishment in addition to the average rates to better understand how interannual differences in recruitment affect population growth. We also separately estimated the effect of plant size on the variance of plant growth ($gvar$) for E^+ and E^- populations of each species.

The IPM projection kernel for each species with or without the endophyte was discretized into a matrix (Yule, Miller & Rudgers 2013), and we calculated the dominant eigenvalue of the discretized matrix to determine the asymptotic population growth rate (λ). The lower integration limit for the model was the smallest observed size (one tiller, $\ln(\text{size}) = 0$), and the upper integration limit was set at 1.1 times the maximum observed size (148 tillers, $\ln(\text{size}) = 5$). To avoid unintentional eviction from the model, we extended the maximum and minimum limits (by 3) and modified the kernel such that all individuals modelled that fell in extended size ranges were treated as demographically equivalent (Williams, Miller & Ellner 2012). This essentially sets a ‘ceiling’ and ‘floor’ in the model by having a class

Table 1. Candidate models of host species demographic functions and model fitting. Superscript + indicates endophyte effect on the intercept (subscript b) or slope (subscript m), and subscript t indicates year. Demographic functions follow those of eqns 2 and 3

Model	<i>P. alsodes</i>		<i>P. sylvestris</i>	
	ΔAIC	AIC Weight	ΔAIC	AIC Weight
Growth $g(y,x)$				
$\text{size}_{t+1} = g_b + g_m * \text{size}_t$	0	0.483	9.1	0.007
$\text{size}_{t+1} = g_b^+ + g_m * \text{size}_t$	2	0.178	0	0.684
$\text{size}_{t+1} = g_b + g_m^+ * \text{size}_t$	1.5	0.218	6.4	0.029
$\text{size}_{t+1} = g_b^+ + g_m^+ * \text{size}_t$	2.7	0.121	1.8	0.280
Flowering $r(x)$				
$\text{logit}(\text{flowering}_{t+1}) = r_b + r_m * \text{size}_t$	8.74	0.005	0.3	0.278
$\text{logit}(\text{flowering}_{t+1}) = r_b^+ + r_m * \text{size}_t$	0.15	0.398	0	0.317
$\text{logit}(\text{flowering}_{t+1}) = r_b + r_m^+ * \text{size}_t$	0	0.428	0.2	0.288
$\text{logit}(\text{flowering}_{t+1}) = r_b^+ + r_m^+ * \text{size}_t$	1.85	0.169	2	0.117
Seed production $f_n(x)$				
$\ln(\text{seeds}_{t+1}) = f_b + f_m * \text{size}_t$	3.55	0.096	1.2	0.195
$\ln(\text{seeds}_{t+1}) = f_b^+ + f_m * \text{size}_t$	3.58	0.094	0.1	0.329
$\ln(\text{seeds}_{t+1}) = f_b + f_m^+ * \text{size}_t$	1.68	0.244	0	0.347
$\ln(\text{seeds}_{t+1}) = f_b^+ + f_m^+ * \text{size}_t$	0	0.566	2	0.129
Survival $s(x)$				
$\text{logit}(\text{survival}_{t+1}) = s_b + s_m * \text{size}_t$	12.2	0.002	13.4	0.001
$\text{logit}(\text{survival}_{t+1}) = s_b^+ + s_m * \text{size}_t$	0	0.713	0	0.673
$\text{logit}(\text{survival}_{t+1}) = s_b + s_m^+ * \text{size}_t$	6.9	0.022	12.8	0.001
$\text{logit}(\text{survival}_{t+1}) = s_b^+ + s_m^+ * \text{size}_t$	2	0.263	1.4	0.325

of 'very big' and 'very small' individuals and includes rare instances of individuals which would otherwise be evicted from the model by exceeding the set integration limits (Williams, Miller & Ellner 2012).

TESTING THE EFFECTS OF ENDOPHYTE SYMBIOSIS ON HOST POPULATION GROWTH

We generated a null expected difference in λ between E^+ and E^- populations ($\lambda_{E^+} - \lambda_{E^-}$) by randomizing endophyte status within each species and refitting demographic functions. This randomization procedure was repeated 10 000 times to estimate 95% confidence intervals for the distribution of the null difference. The null expectation was then compared to the observed difference in λ to determine whether endophyte presence in the population significantly altered λ at a significance level of $\alpha = 0.05$.

IMPERFECT VERTICAL ENDOPHYTE TRANSMISSION

Throughout the life cycle of the host plant, it is possible for the endophyte to be lost from maternal plant to seed through imperfect transmission (Afkhani & Rudgers 2008). To incorporate this phenomenon in our demographic model, we can couple E^+ and E^- IPM kernels into a single model that includes transitions not only between sizes but also between endophyte states. This allows us to predict the equilibrium frequency of E^+ hosts in the population, given the demographic effects of endophyte symbiosis and the rate of endophyte loss. Our approach is akin to the 'megamatrix' approach for multiple, discrete state variables (Pascarella & Horvitz 1998; Yule, Miller & Rudgers 2013). The combined E^-/E^+ model takes the form:

$$\begin{pmatrix} E^-(y)_{t+1} \\ E^+(y)_{t+1} \end{pmatrix} = \begin{pmatrix} \int [p^-(y, x) + f^-(y, x)] dx & \int [(1 - \tau)f^+(y, x)] dx \\ 0 & \int [p^+(y, x) + \tau f^+(y, x)] dx \end{pmatrix} \begin{pmatrix} E^-(x)_t \\ E^+(x)_t \end{pmatrix} \quad \text{eqn 4}$$

The 2×2 megamatrix represents transitions between discrete states of endophyte presence or absence, where the elements contain discretized IPM kernels as described previously, using E^+ or E^- functions, as appropriate. The transition between endophyte states is governed by the vertical transmission rate τ , which is the probability that a seedling from an endophyte-symbiotic parent plant is also endophyte symbiotic (Gundel *et al.* 2008). Because horizontal transmission has not been documented for either species, the probability of transitioning from endophyte-free to endophyte-infected was held at zero. The first eigenvector of the megamatrix predicts the equilibrium distributions of size and endophyte status. The effects of imperfect vertical transmission on host plant population growth and equilibrium endophyte frequency (expected proportion of the population that is symbiotic) were modelled using a range of pE based on field-observed rates.

LIFE TABLE RESPONSE EXPERIMENT

Differences in population growth between the two host species could be caused by differences in 'intrinsic' demography in the absence of symbionts, differences in the effects of symbionts on demography, or both. To quantify the contributions of these processes to the observed difference in λ between species, we used a life table response experiment (LTRE, Caswell 1989). The between-species LTRE decomposed the total difference in λ into the contributions of intrinsic (E^-) demographic coefficients and the endophyte symbiosis effects (the ratio of E^+/E^- for each demographic coefficient). The total difference in λ between spe-

cies reflects the difference in parameter values multiplied by the parameter sensitivity and summed over all parameters that differed between *P. alsodes* and *P. sylvestris* populations (Caswell 2001). We calculated the midpoint sensitivities of intrinsic demography and endophyte effect parameters using the mean megamatrix of *P. alsodes* and *P. sylvestris* as the reference model (Caswell 2001), including the average pE for all host species across all years. Sensitivities were estimated numerically by applying a uniform perturbation, and taking the ratio of the change in λ to the magnitude of the perturbation (0.001) (Ellner & Rees 2006). The LTRE included the vertical transmission rate as a demographic parameter that differed between species. We used vertical transmission rates measured in the laboratory experiment (*P. alsodes* $99.9 \pm 7.6\%$ SE, $N = 81$ seedlings; *P. sylvestris* $16.5 \pm 4.7\%$ SE, $N = 126$) for each host species in the megamatrix.

Results

ENDOPHYTE EFFECTS ON HOST LIFE STAGES

The effects of endophyte symbiosis differed between host life stages and species (Table 2). Endophyte symbiosis increased *P. sylvestris* growth consistently across sizes, had little effect on flowering probability or seed production, and increased survival, especially at small sizes (Fig. 1). In contrast, *P. alsodes* in symbiosis with the endophyte experienced no change in growth, but instead showed a size-dependent decrease in the probability of flowering, an increase in seed production at large sizes, as well as an increase in survival across all sizes (Fig. 2).

Endophyte symbiosis had no significant effect on *P. sylvestris* or *P. alsodes* seedling establishment ($\chi^2_{18} < 0.01$, $P = 0.97$, and $\chi^2_{16} = 3.40$, $P = 0.07$, respectively), but establishment strongly varied among years ($\chi^2_{43} = 9.16$, $P = 0.027$, and $\chi^2_{31} = 19.82$, $P < 0.001$, respectively). There was no significant endophyte status by year interaction effect on the probability of seedling establishment for either species ($\chi^2_{43} = 1.38$, $P = 0.71$, and $\chi^2_{31} = 2.38$, $P = 0.50$, respectively).

ENDOPHYTE EFFECTS ON HOST POPULATION GROWTH

For both host species, endophyte symbiosis significantly affected population growth: the observed difference between E^- and E^+ populations (at average rates of seedling establishment) fell outside the null expectation using randomized endophyte assignments ($P < 0.05$). Endophyte symbiosis increased projected stable population growth rates for both host species. At average seedling establishment probabilities, E^+ populations of the common host *P. sylvestris* were projected to grow 32% faster than E^- populations ($\lambda^+ = 1.43$ and $\lambda^- = 1.11$). For the rare host species *P. alsodes*, E^- populations were projected to decline at average seedling establishment probabilities ($\lambda^- = 0.90$), whereas endophyte symbiosis increased population growth by 18% ($\lambda^+ = 1.08$), resulting in population persistence.

Table 2. Descriptions and fitted parameter values for demographic functions, with pE reflecting the average rate observed in the field across years

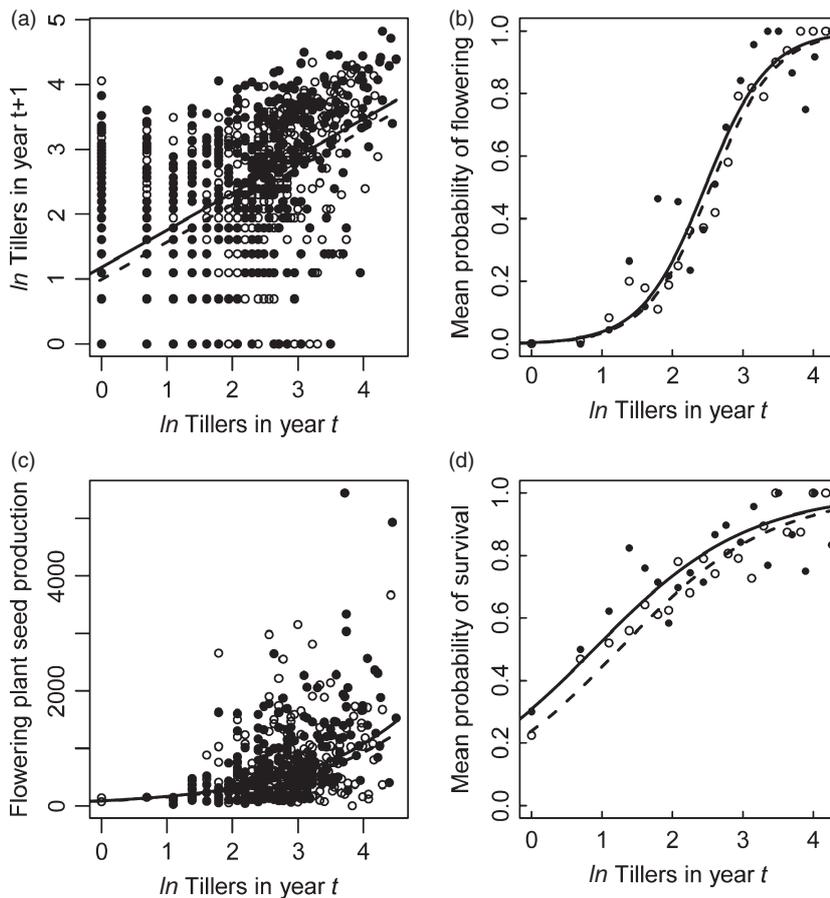
Parameter	<i>P. sylvestris</i>		<i>P. alsodes</i>		Description
	E^-	E^+	E^-	E^+	
s_b	-1.16	-0.81	-0.56	-0.13	Survival intercept
s_m	0.93	0.91	0.46	0.47	Survival slope
g_b	0.99	1.18	1.11	1.12	Growth intercept
g_m	0.58	0.57	0.51	0.50	Growth slope
$gvar_b$	0.93	1.19	0.95	0.71	Growth variance intercept
$gvar_m$	0	-0.12	0	0.22	Growth variance slope
r_b	-5.56	-5.46	-5.09	-5.37	Flowering intercept
r_m	2.19	2.22	2.17	2.04	Flowering slope
f_b	4.45	4.50	3.76	3.36	Seeds intercept
f_m	0.60	0.62	0.68	0.88	Seeds slope
μ	0.099	0.099	0.063	0.063	Mean seedling size
pE	0.014	0.014	0.006	0.006	Probability of establishment
τ		0–1		0–1	Transmission rate*

*Varied from 0 to 1.

We also modelled λ across the range of possible seedling establishment rates documented in the field, and the qualitative pattern remained consistent, with projected λ s increasing as seedling establishment increased (Fig. 3). However, even under the highest observed values of seedling establishment, E^- populations of *P. alsodes* were predicted to decline through time in the absence of endophyte symbiosis ($\lambda^- = 0.90$).

LIFE TABLE RESPONSE EXPERIMENT

The LTRE analysis showed that intrinsic (E^-) demographic rates and endophyte effects both contributed to the difference in λ between the rare versus common host species under the laboratory-measured vertical transmission scenario, which we measured to be *P. alsodes* $99.9 \pm 7.6\%$ SE, and *P. sylvestris* $16.5 \pm 4.7\%$ SE (Fig. 4). Summed across vital rates, the difference in λ between the two host species was more strongly driven by intrinsic differences in their demography than by differences in endophyte effects. Intrinsic survival, seed production and seedling establishment, all greater for *P. sylvestris*, made the largest contributions to the total difference in λ between *P. sylvestris* and *P. alsodes*. Effects of endophyte symbiosis on both host species demographic rates were similar in magnitude, but occurred through different demographic rates (increased growth and flowering in *P. sylvestris*; increased survival and seed production in *P. alsodes*). These

**Fig. 1.** Fitted demographic functions for *Poa sylvestris* in (a) growth, (b) flowering, (c) seed production and (d) survival. Observed data for endophyte-symbiotic and non-symbiotic populations are filled (E^+) and open (E^-) points, respectively. Fitted functions are represented in solid (E^+) and dashed (E^-) lines.

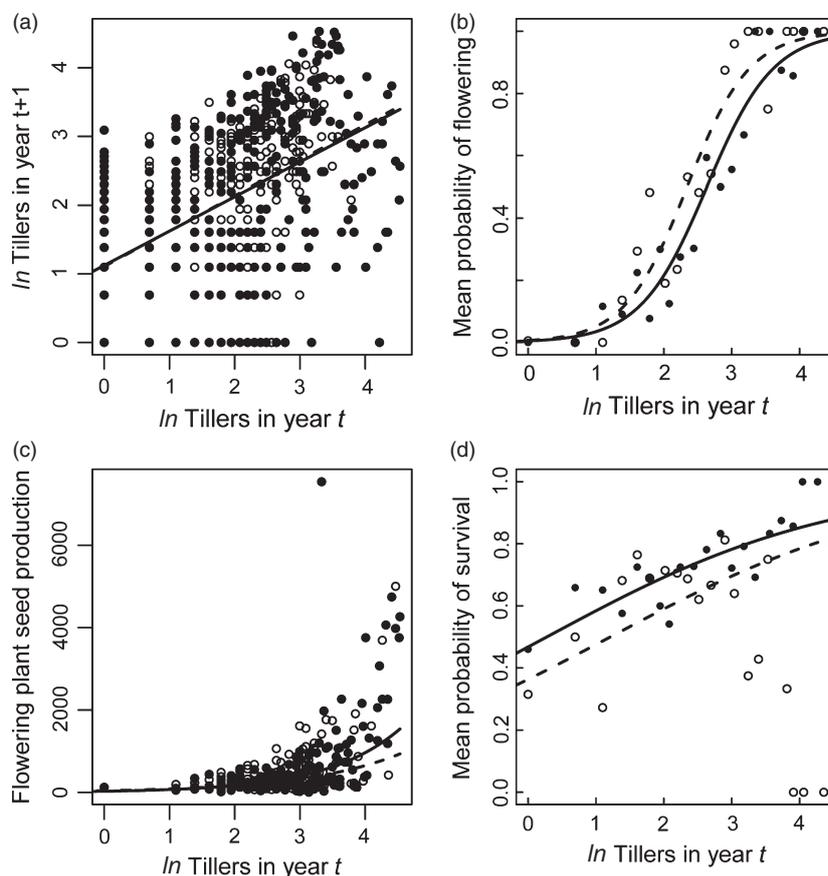


Fig. 2. Fitted demographic functions for *Poa alsodes* in (a) growth, (b) flowering, (c) seed production and (d) survival. Observed data for endophyte -symbiotic and non-symbiotic populations are filled (E^+) and open (E^-) points, respectively. Fitted functions are represented in solid (E^+) and dashed (E^-) lines.

differences in endophyte symbiosis effect between host species together summed to close to zero, showing little contribution of difference in endophyte effect combined across host demographic rates to the difference in λ between hosts. The laboratory transmission rates showed low levels of vertical transmission in *P. sylvestris* and perfect vertical transmission in *P. alsodes*. The contribution of the vertical transmission rate to the difference in λ reflected the decrease in projected λ for *P. sylvestris* due to loss of endophyte symbiosis, which decreased its strong advantage in intrinsic demography.

ENDOPHYTE PERSISTENCE IN HOST POPULATIONS

We found that seedling establishment interacted with endophyte transmission rate to determine equilibrium endophyte persistence (Fig. 5). For both host species, the general pattern held that as vertical transmission rates increased, the predicted λ s and equilibrium endophyte frequencies for host populations increased. However, this relationship was not linear. Our model results showed a threshold vertical transmission rate below which the endophytes went extinct: below the threshold, λ matched the value based solely on E- demography. However, above the threshold vertical transmission rate, there was a positive, linear, relationship between equilibrium endophyte frequency and vertical transmission (Fig. 5). For both host species, the threshold transmission rate approached zero at the lowest observed levels of seedling establishment

and increased as pE increased (Fig. 5). Thus, a greater probability of seedling establishment increased the vertical transmission rate necessary to keep endophytes in the host population. At any given probability of seedling establishment, the projected threshold transmission rate was lower for *P. sylvestris* than *P. alsodes*, which resulted in a higher equilibrium endophyte frequency in *P. sylvestris* compared to *P. alsodes* under less than perfect transmission.

Discussion

To our knowledge, this study was the first to tease apart the effects of symbiosis and intrinsic host demography on host relative abundance. Our results revealed several novel patterns. First, endophyte symbiosis increased host population growth, consistent with prior studies (Rudgers *et al.* 2012; Yule, Miller & Rudgers 2013). However, the net benefit of symbiosis was reflected through different vital rates in the rare versus common host species, and there was a slight cost of endophyte symbiosis to the rare host. Secondly, endophyte symbiosis was crucial for the rare host to maintain population growth at above replacement, whereas the common host was projected to increase with or without endophyte symbiosis. However, intrinsic differences in demography, independent of endophyte symbiosis, contributed more to the difference in projected population growth rates than did differences between host species in the effects of endophyte symbiosis. Thirdly, seedling establishment was a crucial demographic

transition and interacted with the vertical transmission rate of endophytes from maternal plants to seeds in nonlinear ways that affected both host and symbiont population growth. Moreover, lower rates of vertical transmission of the endo-

phyte in the common host compared to the rare host decreased the projected difference in population growth between the two host species.

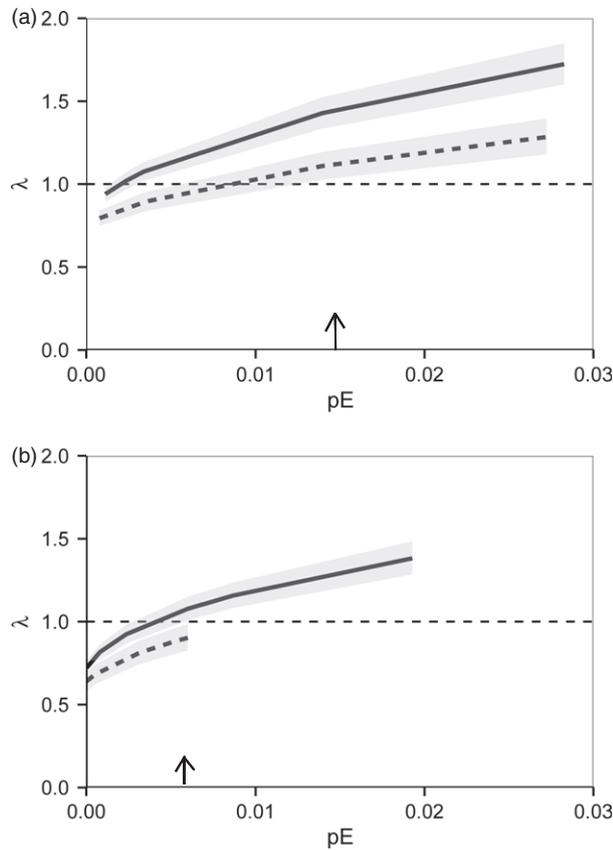


Fig. 3. Projected population growth rates (λ) for E^+ (solid) and E^- (dashed) for (a) *Poa sylvestris* and (b) *Poa alsodes* across range of observed probabilities of establishment (pE) for each population. Shaded areas represent 95% bootstrap CI; arrows indicate average pE for each species. While the range of pE observed in the field differed between E^- and E^+ populations within each species, the difference in means was not statistically significant in either species.

EFFECTS OF ENDOPHYTE SYMBIOSIS ON HOST DEMOGRAPHIC RATES AND POPULATION GROWTH

Results for these two *Poa* species differ from prior grass–endophyte symbioses that have been examined and thus expand the range of observed demographic effects of endophyte symbiosis. Endophyte symbiosis increased survival, as well as the overall population growth of both hosts, but its effects on other host vital rates differed between the two host species we examined. Others have also found combinations of costs and benefits in vertically transmitted endophyte–host interactions. For example, endophyte symbiosis was found to decrease survival but increase reproduction in hosts *Agrostis hyemalis* and *Cinna arundinacea* (Rudgers *et al.* 2012; Yule, Miller & Rudgers 2013), and increase reproduction and growth in *Festuca arizonica* (Faeth 2009). These findings differ from our results, where the cost of endophyte symbiosis was to reproduction (rare host only) and the benefits to survival (both hosts) and growth (common host only). These species-specific effects of endophyte symbiosis could be related to differences in host life history strategies and trade-offs in the host species.

The most likely mechanism by which endophyte symbiosis enhanced host plant growth and survival in our study is herbivore deterrence. Previous work on the plants of these two species showed a 70% and 72% increase (*P. alsodes* and *P. sylvestris*, respectively) in insect herbivory on E^- compared to E^+ plants in laboratory trials (Crawford, Land & Rudgers 2010). In addition, surveys of the field experimental populations studied here showed up to four times more leaf area damaged in E^- *P. alsodes* plants compared to E^+ plants, and over three times more in E^- *P. sylvestris* plants (K. Crawford, J. Land & J. Rudgers, unpubl. data). These herbivory studies all focused on adult plants. However, as seedling establish-

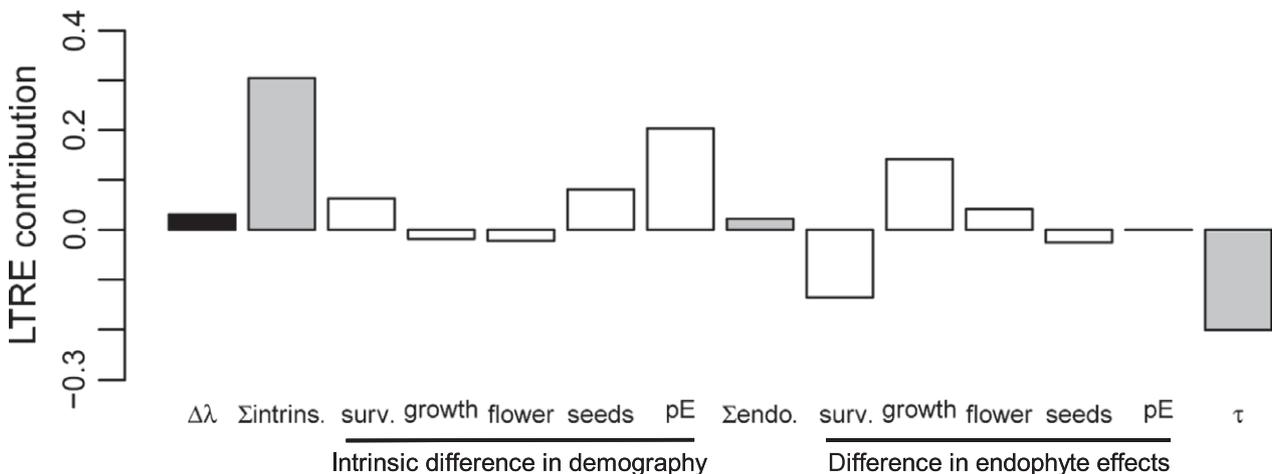


Fig. 4. Contribution of each demographic rate to the difference in λ between *Poa sylvestris* and *Poa alsodes* populations ($\Delta\lambda = \lambda_{P. sylvestris} - \lambda_{P. alsodes}$, in black). Sums of the subsets of contributions reflecting intrinsic demographic differences only (Σ intrinsic.), the effect of endophyte symbiosis only (Σ endo.), and the effect of different vertical transmission rates (τ) are in grey. Individual contributions through each vital rate are in white.

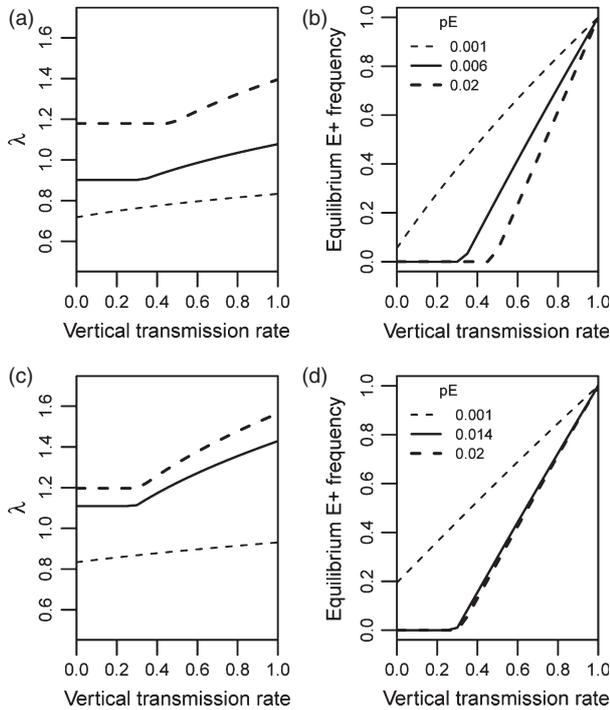


Fig. 5. The effects of imperfect transmission on (a, c) host population growth and (b, d) equilibrium endophyte frequency in the host population. Model projections for *Poa alsodes* in (a) and (b), and *Poa sylvestris* in (c) and (d). Effects of imperfect transmission modelled at three levels of pE . The low and high levels chosen are the same and biologically feasible for both host species. The middle pEs are different for each species and reflect the average probability of seedling establishment observed in the field.

ment did not significantly differ between E^+ and E^- plants in our study, it is unlikely that endophyte-mediated differences in herbivory to early seed or seedling stages drive symbiosis outcomes at the population level for these species.

RELATIVE EFFECTS OF ENDOPHYTE SYMBIOSIS VERSUS INTRINSIC HOST DEMOGRAPHY ON THE DIFFERENCE IN POPULATION GROWTH BETWEEN RARE AND COMMON PLANTS

Demographic models are necessary to gain insights into the population-level consequences of symbioses due to known shifts in interaction outcomes throughout host ontogeny. However, only a handful of studies thus far have utilized this tool to compare rare and common species (e.g. Byers & Meagher 1997; Esparza-Olguín, Valverde & Mandujano 2005; Münzbergová 2013), and none incorporated the potentially strong effects of microbial symbiosis. Using size-structured IPMs, we found that the more common species *P. sylvestris* had a higher projected population growth rate in comparison with its rarer congener *P. alsodes*. This was true in comparing both endophyte-symbiotic and endophyte-free populations. However, when the different effects of endophyte symbiosis on each host were combined to investigate their overall contribution to the difference in host population growth, the contribution of symbiosis was small relative to intrinsic differences between the species. This result suggests that the

common host is projected to grow at a faster rate, not because it benefits more from endophyte symbiosis compared to the rare host, but because of its intrinsic demographic advantage.

The higher population growth of the common species was driven by its higher probabilities of seedling establishment, seed production and survival compared to the rare plant. Previous work comparing rare and common congeners has also found greater probability of survival to reproductive size in *Calochortus* spp. (Fiedler 1987). Similarly, in a demographic analysis of *Neobuxbaumia* spp., the greatest contribution to the greater λ of the common species was attributed to higher recruitment (Esparza-Olguín, Valverde & Mandujano 2005). Our study only focuses on a single pair of rare and common species, so the results cannot be generalized to all common and rare species comparisons. However, the results of our study add the new dimension of symbiotic interactions to this existing work. As additional demographic studies accumulate in the literature, it may become possible to detect general patterns in the critical demographic transitions and ecological interactions that determine plant species' relative abundance.

Of all the vital rates, the probability of seedling establishment was the largest contributor to the higher population growth projected for the common plant, highlighting seedling establishment as a key demographic transition that determines the rarity of *Poa* in our study area. Observed seedling establishment varied widely between years in the study and is likely related to interannual variation in climate. For example, the lowest seedling establishment occurred in 2012, during a drought of nine consecutive months of above-average temperatures and six consecutive months of below-average precipitation in Indiana (Indiana State Climate Office 2013). Data collection for this study is still ongoing and as more data accumulate, future modelling efforts could include stochastic demographic models to assess the effects of climate variation.

Our study of a single pair of rare and common host species supports the hypothesis that it is the intrinsic advantage in demography that drives the dominance of the common host species, but that rare species can depend on symbionts for population persistence. In our model projections, endophyte-free populations of *P. alsodes* did not reach $\lambda \geq 1$ even under the most favourable seedling establishment scenarios. Only when it was symbiotic with its endophyte partner did the model predict population growth at or above replacement ($\lambda \geq 1$). However, a worse-than-average year for seedling establishment or less-than-perfect transmission resulted in projected population decline for *P. alsodes*, which likely contributes to its rarity in the study region. In Indiana, where this study took place, *P. sylvestris* occurs commonly whereas *P. alsodes* is listed as 'rare' (USDA and NRCS 2013). The state of Indiana is situated close to the western edge of the geographic distribution of *P. alsodes*, whereas it is close to the centre of the distribution of *P. sylvestris*. Our results suggest the hypothesis that *P. alsodes* suffers in intrinsic demography compared to *P. sylvestris* due to their relative positions in their respective ranges. However, the benefits of endophyte symbiosis allowed *P. alsodes* to persist at our study site. Previous theory has predicted that facilitative inter-

actions could expand the fundamental niche of a species (Bruno, Stachowicz & Bertness 2003), and others have found symbiosis to expand host niches (Joy 2013). Additional demographic studies on such rare and common species pairs will be able to test the generalizability of this hypothesis for plants as well as animal hosts of beneficial symbionts.

DO RARE AND COMMON HOSTS DIFFER IN PREDICTED LEVELS OF ENDOPHYTE PERSISTENCE, AND HOW DO VERTICAL TRANSMISSION RATES ALTER PROJECTED ENDOPHYTE AND HOST POPULATION GROWTH?

In both host species, the probability of seedling establishment interacted with endophyte symbiosis to change equilibrium rates of endophyte frequency. In our models, increased seedling establishment led to an increase in the minimum vertical transmission rate required for persistence of endophyte symbiosis. The existence of a minimum vertical transmission rate for endophyte persistence is predicted by theory (Gundel, Rudgers & Ghersa 2011) and has been demonstrated in other grass–endophyte species (Yule, Miller & Rudgers 2013). The threshold that we uncovered reflects the level of association between plants and endophytes where the net fitness benefits are sufficient to compensate for endophyte loss due to imperfect transmission, resulting in increased population growth for both host and endophyte. Higher levels of seedling establishment increase the minimum vertical transmission rate, and more generally decrease equilibrium endophyte frequency, because seedling establishment enhances E^- recruitment, thus amplifying the consequences of imperfect transmission.

The rare host, *Poa alsodes*, had higher minimum vertical transmission rates at any given seedling establishment probability than did the common host. In other words, a higher level of endophyte vertical transmission was required for the rarer *P. alsodes* to maintain the symbiosis, given its demographic costs and benefits. This result is in line with the higher costs we found of endophyte symbiosis in the rare host, which was balanced by higher levels of vertical transmission. This pattern was also reflected in our surveys of local populations where endophytes were detected in 92–100% of *P. alsodes* sampled, and only 69–86% of *P. sylvestris*. Using vertical transmission rates from maternal plant to seedling assessed in the laboratory, our models projected equilibrium endophyte frequencies of 100% in *P. alsodes* and 0% in *P. sylvestris* populations. While the discrepancy between model predictions and field surveys could be explained by disequilibria in the field populations, it is more likely that we underestimated *P. sylvestris* vertical transmission rate in the laboratory experiment. For example, it is possible that surface sterilization and laboratory conditions for germination facilitated the germination and establishment of endophyte-free seedlings, which would never be realized under field conditions, thus biasing the estimate of (realized) vertical transmission for the population. Regardless, the lower vertical transmission rates found in the laboratory and simulated by our models of the more common *P. sylvestris* subsequently decreased the projected difference in population growth rates of rare and common hosts.

While we did not detect any significant demographic costs of endophyte symbiosis to the common host, endophyte symbiosis still exerts a carbon drain on host plants (Thrower & Lewis 1973). Both the costs of endophyte symbiosis and imperfect transmission are key reasons why natural endophyte frequencies are not at 100% (Gundel *et al.* 2008).

Conclusion

We found support for the hypothesis that rare species can be maintained in communities by their associations with beneficial symbionts. However, the different fitness benefits of endophyte symbiosis to rare versus common host plants did not contribute substantially to the difference in host population growth rates. Instead, intrinsic demographic advantage was the main driver behind the dominance of the common host species, and asymmetry in vertical transmission rates decreased the projected difference in population growth rates between host species more than expected based on intrinsic demography alone. This is the first time that the relative effects of symbiosis and host demography in driving host population dynamics have been evaluated. We conclude that understanding the interactions among seedling establishment, vertical transmission rates and host species demography are critical for determining population-level outcomes for both host and symbiont species. Our results demonstrate the importance of microbial symbionts in driving population dynamics of host plants, as well as the utility of a demographic perspective for generating new insights into how plant–symbiont interactions vary across host life cycles and contribute to the different life history strategies of rare versus common species.

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Data accessibility

Data deposited in the Dryad repository: <http://dx.doi.org/10.5061/dryad.nf515> (Chung, Miller & Rudgers 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. The effects of heat treatment on endophyte frequency and germination rates of *Poa* seeds.

Figure S1. Elasticities of λ to size transitions for (a, c) E^+ and (b, d) E^- populations of (a, b) *P. sylvestris* and (c, d) *P. alsodes*.