Linking transient dynamics and life history to biological invasion success

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Summary

1. Upon arriving in a novel environment, invading populations are likely to be small and far from a stable stage structure. This unstable stage structure can cause transient (short-term) population dynamics to differ greatly from asymptotic (long-term) dynamics. Because the persistence of small populations depends heavily on population growth rate, short-term dynamics may strongly influence the viability of invading populations.

2. We used published matrix population models to study the dynamics of small 'invading' populations for 105 plant species spanning a range of life histories, including species classified as both invasive and non-invasive. We simulated the matrix population models to estimate the effect of transient dynamics on population viability (i.e. potential invasiveness) after a hypothetical seed dispersal event into a novel environment. We then evaluated the predictive power of transient and long-term population growth rates to explain variation in population viability and identified the life-history correlates of population dynamics that best explained establishment success.

3. Transient and long-term population growth rates were positively but independently correlated with population viability across species. Minimum transient density (minimum population density attained *en route* to a stable stage structure) was the best transient predictor of population viability. This suggests that avoidance of severe short-term population declines is more important during establishment than either the rate of decline or transient ability to increase in density following a decline.

4. Despite a negative correlation between transient density and fecundity, species with high fecundity had disproportionately favourable transient dynamics and higher long-term population growth rates, resulting in higher population viability. Together, these results suggest that highly fecund species are better equipped to overcome the early effects of demographic stochasticity in the establishment phase than less fecund species and help explain the common empirical finding that species invasiveness is correlated with fecundity.

5. *Synthesis.* Transient and long-term population dynamics are independent predictors of demographic performance that influence the viability of invading (i.e. small, unstable) populations subjected to strong effects of demographic stochasticity. Greater long-term population growth rates and disproportionately favourable transient dynamics may account for the commonly observed invasiveness of highly fecund species. Given the strong dependence of population viability on population growth and the wide range of transient responses among species, transient analysis may provide critical insights into the demographic correlates of biological invasion potential.

Key-words: demographic stochasticity, establishment, extinction risk, life history, matrix population models, plant population and community dynamics, population viability, short-term dynamics, stage structure, trade-offs

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Introduction

A constellation of biotic and abiotic processes determine the capacity of a population to invade and ultimately persist in a novel environment. Population performance may be simultaneously affected by resource availability and biological interactions, both of which may be tempered by environmental processes including climate and disturbance regimes (Davis, Grime & Thompson 2000; Shea & Chesson 2002; Allington *et al.* 2013). These pressures form the basis for many key concepts in classical invasion biology (reviewed in Catford, Jansson & Nilsson 2009) and, while some or all of these processes may contribute to successful establishment of an invading population, all invasibility criteria require that the invading population has a positive growth rate from low-density conditions (Chesson & Ellner 1989; Shea & Chesson 2002).

The ecological and economic costs of biological invasions (Pimentel *et al.* 2000; Pimentel, Zuniga & Morrison 2005) create a pressing need to understand the mechanisms responsible for successful establishment of invading population. Factors often associated with successful invasion include propagule pressure, invasion history and physiological tolerance (Colautti, Grigorovich & MacIsaac 2006; Simberloff 2009). Demographic characteristics associated with life-history strategies may play a role in invasion through their effects on propagule pressure and reproductive capabilities (Buckley *et al.* 2005; Simberloff 2009). The timing of invader introduction into the novel habitat as well as stochastic processes, both demographic and environmental, is also thought to play critical roles in establishment success (Crawley 1989; Drake *et al.* 2006).

However, while biological invasions are typically defined as rapid population growth and spread of exotic species in an introduced environment (Richardson *et al.* 2000), a clearer understanding of the invasion process can illuminate a much wider array of ecological processes. For example, the ability of a rare life-history variant to 'invade' a resident population determines the capacity for life-history evolution (Metz, Nisbet & Geritz 1992). Stable coexistence is only possible if low-density populations of multiple species can mutually invade resident populations of the others (Chesson & Ellner 1989). The degree to which a native species can 'invade' and colonize novel habitats at its range limit influences the capacity for range expansion and the ability to cope with climate change (Thomas 2010). In the remainder of this paper, we therefore consider invasion in the broadest sense: the growth of low-density populations in novel environments, irrespective of geographic source (native vs. exotic), long-term population abundance (rare vs. abundant) or impacts on other sympatric species (benign vs. harmful).

After initial dispersal into a novel environment, invading populations are likely to be small and far from a stable stage structure. Both of these circumstances can impose significant barriers to successful establishment. First, extinction risk due to demographic stochasticity (i.e. variation in population growth rate due to random survival and reproduction outcomes among individuals) is highest for small populations and might thus function as an important filter that prevents invading species from successfully establishing in otherwise suitable environments (Lande 1988; Snyder 2003; Drake *et al.* 2006). Secondly, the stage structure of a population provides the demographic basis for an increasingly appreciated source of variability in population performance known as transient dynamics (reviewed in Stott, Townley & Hodgson 2011).

Although the well-known finite rate of increase (λ) describes the long-term performance of a population once the stable stage structure is achieved (i.e. asymptotic conditions), populations with unstable stage structure typically first undergo a period of transient dynamics that can differ markedly from long-term dynamics (Fig. 1; Koons, Holmes & Grand 2007; Stott, Townley & Hodgson 2011; Ellis 2013). Transient dynamics resulting from initially unstable stage structure can cause drastic increases and/or decreases in population abundance *en route* to a stable stage structure and long-term growth rate. In general, departures from a stable stage distribution may be most extreme and common in newly colonized areas (McMahon & Metcalf 2008; Ezard *et al.*
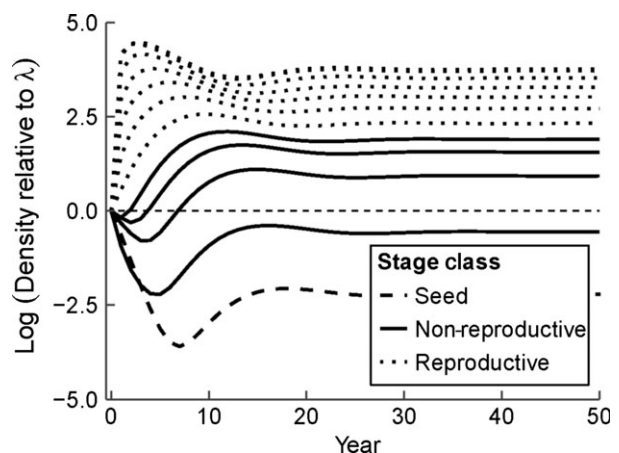

Fig. 1. Example of transient population dynamics for the invasive tree *Sapium sebiferum* (L.) Roxb. (Euphorbiaceae; Renne 2001): a stage-structured population with 1 seed stage, 4 vegetative stages and 7 reproductive stages. Each of the 12 lines represents a unique population growth trajectory resulting from initial conditions in which all individuals were initially placed into a single stage class. The *y*-axis represents (standardized) population density relative to a population growing at its long-term growth rate λ with stable stage structure (dashed line at y = 0; *sensu* Stott, Townley & Hodgson 2011). Negative values indicate that population density is lower than a population growing at λ; positive values indicate density is higher than a population growing at λ. In this example, short-term population growth is much lower than λ when all individuals are initially grouped into the seed stage; relative density at year 10 is over 35 times lower than if the population was growing at λ. This results in persistent negative effects on density (i.e. population inertia; Koons, Holmes & Grand 2007) even after the long-term growth rate is attained at approximately 30 years. Although the dynamics of an invasive species is shown here, most species and populations in this study are classified as non-invasive.

2010). As a consequence, transient growth rates of invading species only rarely approximate asymptotic performance (Koons *et al.* 2005; Williams *et al.* 2011; Crone *et al.* 2013; Ellis & Crone 2013). Thus, invading populations could potentially experience significant extinction risks due to stochastic events if transient growth rates reduce invading populations to (or maintain populations at) low density, despite a high asymptotic growth rate.

The life history of a species, defined as the time, duration and magnitude of important life cycle processes such as growth, reproduction and mortality (Stearns 1992), greatly influences vulnerability to demographic stochasticity (Kokko & Ebenhard 1996; Jeppsson & Forslund 2012), as well as transient dynamics (Koons *et al.* 2005; Koons, Grand & Arnold 2006; Stott *et al.* 2010a,b). For example, Jeppsson & Forslund (2012) used a simulation approach to examine the effect of demographic stochasticity on population viability across a wide range of hypothetical life histories, assuming an initially stable stage distribution. In general, extinction risk due to demographic stochasticity was greater for long-lived species with delayed reproduction and was also positively correlated with fecundity. However, long-lived species with delayed reproduction generally exhibit greater differences between transient and asymptotic dynamics than short-lived species (Koons *et al.* 2005; Koons, Grand & Arnold 2006), which could dramatically alter predicted extinction risk if the stage structure is not yet stable. To date, no study has investigated the interactive consequences of transient dynamics and demographic stochasticity on extinction risk. Given the considerable diversity of plant life histories (Franco & Silvertown 1996; Moles & Westoby 2006; Adler *et al.* 2014), comparative analyses of plant population dynamics are likely to provide key insights into the combined influence of short- and long-term growth rates on population viability.

Drawing from the COMPADRE Plant Matrix Database (Salguero-Gómez *et al.* 2015), we use empirically derived population models to simulate the dynamics of small populations and investigate potential invasive success of 105 plant species spanning a range of life histories, including species classified as both invasive and non-invasive. We simulate population viability for each species after initiating populations as seeds, representing a dispersal event into an uncolonized environment. We then evaluate the ability of short- and long-term growth rates to explain variation in population viability and determine the life-history correlates with population dynamics that best explain the ability to overcome demographic stochasticity (i.e. potential invasiveness). Given the strong link between population growth rate and extinction risk, we hypothesize that small populations with highly positive transient growth rates should quickly overcome the early effects of demographic stochasticity and experience much higher population viability than populations with small or negative transient growth rates. Our specific objectives were to (i) evaluate interspecific variation in transient dynamics resulting from initiating populations as seeds, (ii) quantify the effects of transient dynamics and long-term population growth rates on the ability of low-density populations to overcome demo-

graphic stochasticity and (iii) determine the life history characteristics that best explain interspecific patterns in short- and long-term population growth. Together, these objectives are designed to quantify the importance of transient dynamics for early establishment success and to provide a predictive framework for identifying key demographic features of potential invader species.

Materials and methods

To evaluate the joint influence of transient dynamics and life history on the viability of small populations, we used the COMPADRE Plant Matrix Database version 3.2.0 (Salguero-Gómez *et al.* 2015; www.compadre-db.org). In its newest version, COMPADRE contains matrix population models and associated covariate information for 735 plant species. Because of the significant role of propagules in biological invasions (Lockwood, Cassey & Blackburn 2005; Colautti, Grigorovich & MacIsaac 2006; Simberloff 2009), we restricted our analyses to time-invariant matrix population models where seed stages were explicitly represented. To investigate the role of demographic stochasticity as a filter on otherwise viable populations, we further restricted our analyses to populations with an estimated positive long-term population growth rate, a necessary criteria for invasion (i.e. log (λ) > 0, where λ is the dominant eigenvalue of the matrix population model; Caswell 2001). We only selected matrices that were ergodic and irreducible (Stott *et al.* 2010a,b), and modelled on an annual time step. We also excluded matrices with extremely high and possibly unrealistic growth rates (log(λ) > 2; n = 1). Finally, for species represented multiple times through different publication sources in COMPADRE that met the above criteria, we preferentially selected mean matrices based on multiple years and sites of demographic information and those based on unmanipulated populations or control treatments. Our selection criteria yielded a total of 105 species and associated time-invariant matrix population models for analysis (see Table S1, Supporting Information for a complete list of species used in analyses and associated references). Our final list included projection matrices for 91 non-invasive species and 14 species classified as exotic invasives. For the invasive species included in our analysis, 11 matrices were derived from invasive populations, while 3 were derived from populations in the species' native range. Yet, we emphasize that our goal was not to directly compare the dynamics of invasive and non-invasive species, but rather to study the early dynamics and viability (i.e. 'potential invasiveness') of small populations across a wide range of life histories.

SIMULATION MODELS AND POPULATION VIABILITY

We used a series of population simulations to measure transient dynamics caused by introducing populations as seeds (objective 1) and to quantify the relationship between population dynamics and viability (objective 2), defined as the probability of avoiding extinction due to demographic stochasticity. Because some species had multiple seed stages represented in the matrix population model (e.g. dormant stages), we first determined the seed stage class with the largest stable stage abundance following methods described in Caswell (2001, p. 87), assuming that this stage represented the most likely dispersal stage. This single seed stage was used to create initial conditions and evaluate the relationship between transient dynamics and population viability. For each species, we initialized simulations with all individuals grouped into the single seed stage class (e.g. $\mathbf{n}_0$ = [10,0,0,0,0], where $\mathbf{n}_0$ is the population abundance vector at the

beginning of the simulation), representing a hypothetical stage-specific dispersal event into an uncolonized environment. We initialized simulations at one of four initial abundances: 1, 10, 100 or 1000 seeds, allowing us to quantify the effect of initial abundance on population viability.

Population abundance across each simulation was projected as:

$$\mathbf{n}_t = \mathbf{A} \cdot \mathbf{n}_{t-1} \qquad \text{eqn 1}$$

where $\mathbf{A}$ is the species-specific matrix population model, and $\mathbf{n}_t$ represents the vector of stage abundances at time t. We incorporated demographic stochasticity by treating stage-specific fecundity as a Poisson random process with expectation F_k and stage-specific survival and growth as a binomial random processes with expectation S_k and G_k. Actual stage abundances therefore take on integer values and have the potential to reach values of zero (hence, total abundance can also go to zero). We ran each simulation for 500 years, enough time steps to reach asymptotic conditions in the absence of environmental stochasticity (DT Iles unpublished data), and determined whether the population was extinct (i.e. $N_{500} = 0$) at the end of the simulation. This process was simulated 1000 times to calculate population viability for each species under each set of initial conditions (i.e. proportion of simulations with nonzero abundance at 500 years; Morris & Doak 2002).

CALCULATION OF TRANSIENT DYNAMICS

Following Stott, Townley & Hodgson (2011), for each species, we calculated a set of transient density metrics $\left(T_t^{\text{seed}}\right)$ resulting from introductions of seeds, using:

$$T_t^{\text{seed}} = \log\left(\frac{N_t^{\text{seed}}}{N_t^{\lambda}}\right) \qquad \text{eqn 2}$$

where N_t^{seed} represents the total abundance of a population at time t that began with all its individuals grouped into the seed stage, and N_t^{λ} represents the total abundance of a population at time t that began at a stable stage structure. Under this framework, transient density describes the proportional density of a population with a specific initial stage structure (in this case, beginning as seeds) relative to the density of a population with stable stage structure growing at its asymptotic growth rate, λ (Fig. 1). Positive values indicate that transient dynamics increase population density relative to a population growing at λ under stationary conditions, while negative values indicate that transient dynamics depress population density relative to λ. Note that because the projection models used in this study are time-invariant and density-independent, metrics of transient dynamics for populations do not depend on initial density.

Transient dynamics can be evaluated over any relevant time horizon (Stott, Townley & Hodgson 2011). In this study, we considered several time horizons that are potentially relevant for a population to overcome demographic stochasticity: relative transient density after 1, 3, 5, 10, 50 and 100 years, as well as the maximum and minimum transient density attained across the 500 year simulation (T_1^{seed}, T_3^{seed}, T_5^{seed}, T_{10}^{seed}, T_{50}^{seed}, T_{100}^{seed}, $T_{\text{Max}}^{\text{seed}}$ and $T_{\text{Min}}^{\text{seed}}$, respectively). These metrics were then used as potential explanatory variables for population viability.

EFFECT OF TRANSIENT AND LONG-TERM DYNAMICS ON POPULATION VIABILITY

To explore the effects of population dynamics on population viability, we logit-transformed ($\log(y/[1-y])$) estimates of population viability

from simulation results (which were constrained between 0 and 1), facilitating the use of linear models for fitting and interpreting the effects of short- and long-term population growth. We ensured logit-transformed data did not contain undefined values by adding or subtracting a small value (0.001) to population viability values of 0 and 1, respectively (Warton & Hui 2011; Peterson *et al.* 2013).

To allow for comparison of a reasonable number of models and to avoid model dredging (Burnham & Anderson 2002), we first parameterized a series of linear models including each one of the eight metrics of seed transient dynamics (T_t^{seed}) as predictors. After determining the best single transient predictor of population viability, we evaluated support for additive effects of initial abundance, log (N_0), long-term population growth rate, $\log(\lambda)$ and the best transient metric, T_t^{seed}. We assessed relative model support using Schwarz's information criterion (SIC; Schwarz 1978), which tends to be more conservative with respect to model complexity than Akaike's information criterion (Akaike 1973; Aho, Derryberry & Peterson 2014). After arriving at a best-supported fixed-effects model, we included a species random-effect to account for unexplained variation in population viability that was not accounted for by other demographic factors.

To directly compare the relative importance of each predictor of population viability in our top model, we re-estimated the regression coefficients associated with each predictor after Z-standardizing each explanatory covariate, resulting in each predictor having a mean of 0 and a standard deviation of 1. Thus, the relative magnitude of regression coefficients in our top model indicated the relative effect of each predictor on population viability.

LIFE-HISTORY CORRELATES OF POPULATION DYNAMICS

Our second objective was to evaluate the ability of key life-history traits to explain interspecific patterns in transient and long-term population growth. We considered four life-history correlates that have been associated with plant invasiveness and known to affect population dynamics and evaluated the ability of these life-history correlates to explain variation in seed transient dynamics and long-term growth rates across species. Life-history variables included in our analysis were as follows: (i) mean life expectancy from the first non-seed stage to eliminate biases associated with uncertainty in seed survival (Baskin & Baskin 2001) with calculations based on Caswell (2001, p. 118–120); (ii) maximum fecundity of reproductive plants (a potentially important proxy for propagule pressure and thus initial density; Moles *et al.* 2004); (iii) matrix dimension, a surrogate for life cycle complexity and known to potentially affect demographic inference, including the magnitude of transient dynamics (Tenhumberg, Tyre & Rebarber 2009; Salguero-Gómez & Plotkin 2010; Stott *et al.* 2010a, b); and (iv) species growth form (annual, herbaceous perennial, succulent, shrub and tree) to account for potential differences in overall life cycle characteristics and resultant population dynamics.

We also recorded the invasive status of species as a binary variable, based on whether the species is considered invasive anywhere in the world. This information was acquired from (i) the published source from which the matrix model was obtained as detailed in COM-PADRE, (ii) the Global Invasive Species Database and/or (iii) USDA Federal and State noxious weed list. In total, only 14 of the 105 species in our analysis were considered invasive by at least 1 of these criteria (Appendix S1). Life-history characteristics and population dynamics of invasive and non-invasive species were highly variable and overlapped broadly. This indicates that the diverse suite of non-invasive species used in this analysis to investigate the mechanisms

responsible for establishment success are likely to represent both problematic (i.e. 'invasive') and benign (i.e. native and exotic 'non-invasive') species.

We conducted a series of pairwise linear regressions on these life-history covariates to evaluate potential multicollinearity. Although several pairwise regressions were statistically significant, R^2 values were generally weak, indicating that life-history covariates were not strongly multicollinear. For example, matrix dimension was positively correlated with both life expectancy and maximum fecundity, though these relationships were not highly predictive ($R^2 = 0.08$ and 0.03, respectively).

Of the 105 species in our data set, 93 species were simultaneously represented in the COMPADRE phylogeny (Salguero-Gómez *et al.* 2015; www.compadre-db.org). We conducted a series of pairwise phylogenetic least square (PGLS) regressions on life-history covariates to examine the potential effects of non-independent ancestry on observed life-history relationships. Estimates of Pagel's lambda, an index of phylogenetic signal in the data, were generally low (<0.05 ± 0.50 95% C.I.) for pairwise trait relationships, though several pairwise relationships did display strong phylogenetic signals. However, we must note that in all of these pairwise phylogenetic regressions, the confidence intervals around Pagel's lambda were extremely broad, indicating a significant degree of uncertainty in these estimates. Given weak multicollinearity among life-history covariates and generally low and highly uncertain phylogenetic relatedness among life-history traits, we used standard linear regressions to separately identify the best life-history predictors of log(λ) and transient dynamics among all 105 species in our database. Results were qualitatively similar using phylogenetic regressions with the smaller subset of species for which a phylogeny was available. We compared support among competing linear models using SIC. We conducted all simulations and statistical analyses using the R statistical programming language (version 3.1.0) and used the ape (Paradis, Claude & Strimmer 2004) and caper (Orme 2013) packages to conduct PGLS analyses.

Results

TRANSIENT DYNAMICS RESULTING FROM INTRODUCTIONS OF SEEDS

Transient dynamics resulting from introductions of seeds varied dramatically across the 105 plant species in our study (Fig. 2). Transient densities were generally lower than if populations were growing at their asymptotic rate λ with a stable stage structure. After introducing populations as seeds, most populations rapidly declined in density relative to λ, owing to mortality of seeds and vegetative plants before reaching reproductive maturity. Only one species (*Orchis purpurea* Huds.; Berg 2002) attained a greater long-term density following an introduction of seeds than if the population was growing at λ. Most populations reached their stable stage structure by year 50 (though note several exceptions; Fig. 2).

EFFECT OF TRANSIENT AND LONG-TERM DYNAMICS ON POPULATION VIABILITY

Population viability of the 105 studied plant species, defined as the probability of avoiding extinction due to demographic stochasticity, was positively correlated with initial abundance
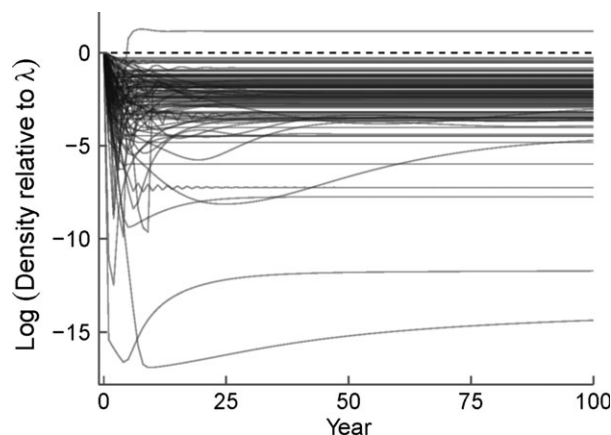

Fig. 2. Transient dynamics following introductions of seeds were highly variable across the 105 species in our study. Each line represents transient dynamics for a single species resulting from initiating the population as seeds. Axes are interpreted as in Fig. 1.

(N_0). Populations initiated from a single seed had extremely low population viability (median = 0.002, range = 0–0.26). Conversely, introductions of 1000 seeds resulted in high viability for most species (median = 0.86, range = 0–1.0), although many species still experienced significant extinction risk (Fig. 3b).

Both transient and long-term dynamics were well-supported predictors of population viability (Tables S2 and S3). As expected, asymptotic population growth rate, log(λ), was positively associated with population viability. Minimum transient density (T_{Min}^{seed}), the minimum population density attained *en rout*e to a stable stage structure, was the best-supported transient population metric (Table S2) and was positively associated with population viability (Fig. 3a). Species invariably had negative values of T_{Min}^{seed} (median = −3.1, range = −16.9 to −0.27; Fig 3c). Because T_{Min}^{seed} is calculated on a log scale, declines in population density relative to λ varied by seven orders of magnitude across species. Furthermore, log(λ) was not correlated with T_{Min}^{seed} ($P = 0.18$, $R^2 = 0.007$), suggesting that short- and long-term growth dynamics were largely independent.

We assessed the relative importance of each predictor of population viability by Z-standardizing the three explanatory covariates in our top model, thereby taking into account both the degree of variance in each predictor and the strength of its effect. Standardized regression coefficients associated with log(N_0), log(λ) and T_{Min}^{seed} were 2.9 (SE = 0.08), 1.4 (SE = 0.21) and 1.5 (SE = 0.21), respectively. The standardized regression coefficients for T_{Min}^{seed} and log(λ) were not significantly different ($P = 0.73$), indicating that short- and long-term dynamics are of similar (but independent) importance for determining population viability.

LIFE HISTORY CORRELATES OF POPULATION DYNAMICS

The best life-history predictors of T_{Min}^{seed} were maximum fecundity of flowering plants and matrix dimension. Maxi-

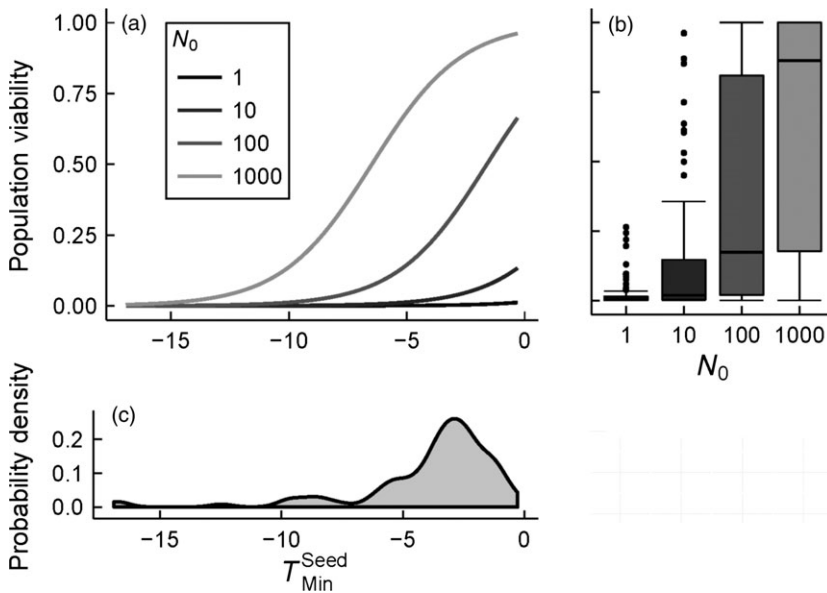**Fig. 3.** The minimum transient population density (T_{Min}^{seed}; on a log scale) resulting from initiating populations as seeds was positively associated with population viability, quantified as the resistance to extinction due to demographic stochasticity. (a) Fitted relationship between T_{Min}^{seed} and population viability across 105 species for four levels of initial population abundance (N_0), based on the best-supported generalized linear model. (b) Distribution of population viability across species for four levels of initial population abundance (N_0). (c) Distribution of T_{Min}^{seed} across species.

mum fecundity was negatively correlated with T_{Min}^{seed}, indicating a trade-off between seed quality and fecundity. Matrix dimension was also negatively correlated with T_{Min}^{seed}. Mean life expectancy and growth form were not significant predictors of T_{Min}^{seed} after accounting for fecundity and matrix dimension. The best predictors of long-term (asymptotic) population growth rate were maximum fecundity and matrix dimension; fecundity was positively correlated with $\log(\lambda)$ while matrix dimension was negatively correlated with $\log(\lambda)$. Mean life expectancy and growth form were not significant predictors of $\log(\lambda)$ after accounting for fecundity and matrix dimension.

TRADE-OFF BETWEEN TRANSIENT DYNAMICS AND FECUNDITY

Assuming initial density is proportional to fecundity, the negative correlation between T_{Min}^{seed} and fecundity (above) implies that initial conditions of founding populations should fall along a continuum. On one end, populations of slow-lived species tend to initiate with a few high-quality seeds (low N_0 and high T_{Min}^{seed}), while at the other end, populations of highly fecund fast-lived species tend to initiate with many low-quality seeds (high N_0 and low T_{Min}^{seed}). To directly explore the implications of this trade-off for invader population viability, we regressed T_{Min}^{seed} against $\log(maximum\ fecundity)$ after Z-standardizing both covariates. The slope of this regression was -0.39 ($P < 0.001$; Fig. 4 grey line). We then compared this 'empirical slope' to the slope of a perfect trade-off (i.e. a population viability isocline) based on the estimated standardized effects of N_0 and T_{Min}^{seed} on population viability (see Effect of Transient and Long-Term Dynamics on Population Viability in Results).

After accounting for random species effects, the main effect of N_0 on population viability was 1.90 times stronger than the main effect of T_{Min}^{seed}; thus, the slope of a perfect trade-off resulting in equivalent population viability was -1.90 (Fig 4 black dashed line). The observed correlation between T_{Min}^{seed}

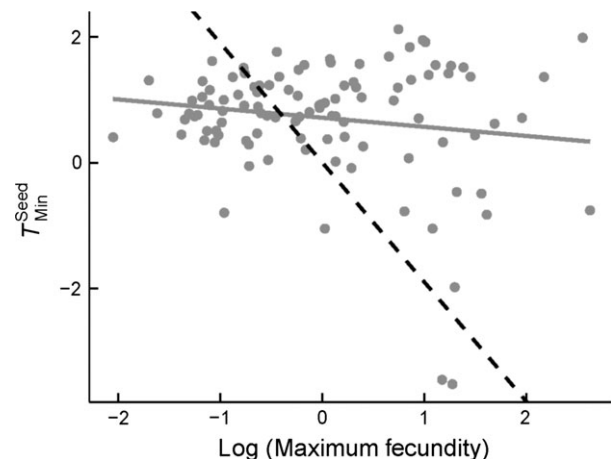**Fig. 4.** Relationship between T_{Min}^{seed} and maximum fecundity of flowering plants (on Z-standardized scales). Each point represents values for a different species. Grey solid line represents empirical relationship between T_{Min}^{seed} and log(fecundity) based on phylogenetic regression (P-value < 0.001, $R_{adj}^2 = 0.14$). Black dashed line represents perfect trade-off resulting in equivalent population viability calculated using standardized regression coefficients and assuming a proportional relationship between fecundity and N_0. Species with higher fecundity have disproportionately high values of T_{Min}^{seed} (i.e. occur above the optimal trade-off line more frequently) than species with lower fecundity.

and fecundity (a proxy for N_0) was nearly five times weaker than the slope of a perfect trade-off, indicating that highly fecund species have disproportionately high values of T_{Min}^{seed}. Thus, fast-lived, highly fecund species are expected to avoid stochastic extinction more readily than slow-lived species through the combined effects of high initial abundance and disproportionately high values of T_{Min}^{seed}.

Discussion

One of the long-standing goals in ecology is to determine the conditions that allow invading populations to achieve positive

long-term population growth rates (Shea & Chesson 2002). Yet even in environments that permit long-term population growth, demographic stochasticity may provide an important barrier to successful invasion by introducing significant extinction risk for small populations (Lande 1988, 1993; Kokko & Ebenhard 1996; Sæther *et al.* 2004; Engen *et al.* 2005; Jeppsson & Forslund 2012). We found that unstable stage structure in founding populations can greatly alter extinction risk if transient population growth reduces invading populations to low density, thereby magnifying and prolonging the effects of demographic stochasticity. Our simulations show that the transient dynamics of the dispersal stage of sexually reproducing plants (i.e. seeds) are highly variable across species, strongly influence population viability, are largely decoupled from long-term dynamics and are correlated with life-history strategies.

Avoidance of severe transient declines in density caused by unstable stage structure was critical for population persistence. Populations beginning from seed stages experienced sometimes > 1 000 000-fold reductions in density before reaching their positive asymptotic growth rate, greatly predisposing these populations to extinction through demographic stochasticity (Fig. 2; Lande 1988; Snyder 2003). Intriguingly, measures associated with rate of population decline (i.e. T_1^{seed} and T_3^{seed}) or the ability to recover from possible initial declines (i.e. T_{100}^{seed} and T_{Max}^{seed}) were not as strongly associated with population viability as T_{Min}^{seed}. Furthermore, these alternative measures were not always highly correlated with measures of maximum population decline (Appendix S2) which is consistent with other studies of transient demography that found measures of short-term population decline are weakly correlated with measures of short-term population gain (Stott *et al.* 2010a,b; Ellis & Crone 2013). Our results therefore demonstrate a rich diversity of patterns among species in the rate, magnitude and ability to recover from declines in density following introductions of seeds.

In general, species with high fecundity experienced greater short-term declines in density than less fecund species. This relationship is likely driven by the well-documented trade-off between seed size (a strong predictor of seedling survival) and seed number (Aarssen & Jordan 2001; Henery & Westoby 2001; Westoby *et al.* 2002; Moles & Westoby 2004). T_{Min}^{seed} represents an omnibus measure of declines in density caused by the dynamics of survival, growth and reproduction following introductions of seeds. Large seeds typically have higher rates of seedling establishment than small seeds, owing to larger nutrient stores that confer the ability to cope with environmental hazards (Westoby *et al.* 2002; Moles & Westoby 2004). Thus, for a given initial density, large-seeded species with low fecundity should be expected to experience smaller transient declines in density than species that produce many small seeds of low quality.

Nevertheless, several recent meta-analyses have suggested that invasive species may generally have higher fecundity (i.e. seed number) than non-invasive species (Pyšek & Richardson 2007; but see Hawkes 2007; Van Kleunen, Weber & Fischer 2010). Furthermore, Hamilton *et al.* (2005) found that the best predictor of species invasiveness in Australia at multiple spatial scales was lower seed mass, which is tightly correlated with seed number (Moles *et al.* 2004) and wind-facilitated dispersal ability (Howe & Smallwood 1982). Similarly, Williamson & Fitter (1996) found a positive association between invasiveness and plant height, which is positively correlated with seed number (Moles *et al.* 2004). In a field comparison of invasive and non-invasive species, Burns *et al.* (2013) found that increased sexual reproduction was a key correlate of species invasiveness. Our study may provide a robust demographic explanation for these findings. Initial density (i.e. propagule number) strongly influences extinction risk (Fig. 2; see also Lande 1988). Yet, propagule number is negatively correlated with subsequent population performance T_{Min}^{seed} (Fig. 4 grey line). Critically, the empirically measured negative correlation between T_{Min}^{seed} and fecundity was much weaker than the slope of a 'perfect trade-off'. This implies that species with high fecundity have disproportionately high values of T_{Min}^{seed} relative to species with low fecundity (Fig. 4), greatly enhancing their relative population viability. Additionally, high fecundity was associated with higher long-term population growth rate, which also increases population viability. Together, these findings are consistent with the common empirical finding that highly fecund species are better equipped to overcome the early effects of demographic stochasticity in the establishment phase than less fecund species.

As a first step towards providing a demographic explanation for patterns of species invasiveness in the literature, the analysis described above assumed that the initial abundance of a founding population was proportional to fecundity (i.e. N_0 is a linear function of seed number). In reality, the shape of the relationship between founding population size and seed number may depend upon seed physiology and dispersal syndrome (Nathan & Muller-Landau 2000). For example, Muller-Landau *et al.* (2008) detected a negative correlation between seed mass and dispersal distance for animal-dispersed species in a tropical forest, and also found that animal dispersal resulted in higher 'clumping' of seeds than other dispersal syndromes. Similarly, 'directed dispersal' of seeds by animal vectors could result in higher founding population abundances than would be expected by chance (Wenny 2001). Together, these patterns should disproportionately increase founding population sizes of small-seeded (and thus highly fecund) species, further strengthening the observed fitness disparity (Fig. 4) between low- and high-fecundity species. Alternatively, Thomson *et al.* (2011) found that dispersal distance was positively correlated with seed mass for unassisted, ballistic and wind-dispersed species. Positive correlations between dispersal distance and seed mass would disproportionately favour the dispersal of large seeds, causing large-seeded (and thus less fecund) species to arrive in greater abundance in novel environments, weakening the observed fitness disparity between low- and high-fecundity species (Fig. 4). Further research into the links between dispersal ability and transient dynamics following dispersal is needed and could provide important insights into variation in biological invasiveness across taxonomic groups and dispersal syndromes.

We found that short- and long-term growth rates for populations are uncorrelated, suggesting two independent axes of demographic variation that can explain establishment success. This is consistent with other studies that found loose correlations between short- and long-term dynamics (Ezard *et al.* 2010; Stott *et al.* 2010a,b; Gamelon *et al.* 2014). While several analyses have suggested that asymptotic and transient sensitivities are often similar (Caswell 2007; Ezard *et al.* 2010; Maron, Horvitz & Williams 2010), there are occasionally large differences between these sensitivity measures (Koons *et al.* 2005). This suggests that perhaps environmental factors that influence long-term persistence can operate somewhat independently of the factors that determine transient dynamics. Thus, while our analysis indicates that short- and long-term dynamics are both important for explaining interspecific vulnerability to demographic stochasticity, research that seeks to evaluate simultaneous responses of short- and long-term growth rates to perturbations across a range of environmental conditions will provide much deeper insights into these joint processes that affect establishment success.

Most previous theoretical and modelling studies of the effects of demographic stochasticity on stage-structured populations have assumed that small populations are at a stable stage distribution, and consequently, that populations are growing at an asymptotic growth rate λ. This assumption may be true for rare species with established populations, as many natural populations appear to be close to their stable stage distribution (Williams *et al.* 2011). However, for small populations that have recently dispersed into novel environments (i.e. biological invasions; McMahon & Metcalf 2008; Ezard *et al.* 2010) or for populations strongly affected by exogenous environmental pressures that affect specific stages (e.g. trophy hunting; Coltman *et al.* 2003), this assumption is questionable. We focused our analyses on the transient dynamics of a single stage class because plant dispersal is generally confined to the seed stage, whether seeds are dispersed naturally or artificially. However, dispersal of asexual clonal propagules (Santamaría 2002) and the transplant of non-seed horticultural plants (Hodkinson & Thompson 1997) are possible. For other biological kingdoms, propagules may often derive from multiple stage classes. In all such cases, founding populations are still likely to be far from a stable stage structure, and transient analysis can be usefully applied to study the resultant dynamics and their consequences. Extensions of our approach to other kingdoms of life could be especially interesting, as greater variation in founding stage structure allows for a much richer variety of transient behaviours following dispersal into a novel environment. Studies that link the drivers of variation in propagule stage structure to resultant transient dynamics will be of interest for metapopulation theory and for applied conservation.

As a first step towards understanding the demographic processes governing the early stages of biological invasions, we took advantage of readily available density-independent models to examine short- and long-term population growth trajectories. Yet, density-dependent feedbacks are a ubiquitous feature of natural populations (Fowler 1981; Harms *et al.* 2000) and can arise from competition with members of either the same species or other species in the community (Chesson 2000). Density-dependent effects can in principle affect any stage class, but may often have especially strong effects on early life cycle transitions (e.g. recruitment and seedling survival; Harms *et al.* 2000). These effects therefore have the capacity to influence estimates of both transient dynamics and asymptotic growth rates (Eager, Rebarber & Tenhumberg 2012). For example, if a density-independent matrix model is fit to data in which density-dependent effects are concentrated on the seed and seedling stages, we should expect more negative estimates of transient growth rates following introductions of seeds (i.e. lower values of $T_{\text{Min}}^{\text{seed}}$) and simultaneously lower asymptotic growth rates than we would find with a density-dependent model.

This concern is especially important for studies designed to explicitly examine differences in population dynamics between invasive and non-invasive populations. The strength of density dependence is likely to vary across a species range, both in the introduced and native environments, owing to spatial variation in ambient population density. Along these lines, McMahon & Metcalf (2008) found that the demography and transient dynamics of several invasive shrubs differed between the invasion core vs. the edge, likely owing to spatial differences in population density and stage structure. Comparative studies of invasive vs. non-invasive species that do not account for density-dependent effects that may be implicit in density-independent projection models may therefore be misleading. In the absence of a balanced sample for comparison and relevant information regarding ambient population density from which each projection matrix was derived, we therefore avoided making potentially misleading comparisons between invasive, non-invasive and native populations. However, the populations used in our study spanned an extremely wide range of life histories, transient responses and asymptotic dynamics that are likely to encompass the range of variation observed both across invasive and non-invasive species, in introduced and native ranges, and at the core and edge of invasions. Given this wide variation, we believe our study provides important insights into the general demographic processes governing biological invasions. Because our study was not designed to compare the dynamics of species' populations that have become invasive vs. those that have not, research that extends our approach to such a comparison will be of theoretical and applied interest.

Here, we have shown that interspecific variation in transient population dynamics caused by unstable stage structure can greatly influence extinction risk of small populations. Given the strong dependence of population viability on growth rate, transient dynamics therefore provide important information about the likelihood of demographic stochasticity to 'filter out' invading populations. However, demographic stochasticity is only one of many factors that influence invasion success, which also include environmental stochasticity (Lande 1988; Simberloff 1988), genetic diversity (Lande 1988; Szűcs *et al.* 2014), dispersal characteristics (Kot, Lewis & Van Den Driessche 1996; Hodkinson & Thompson 1997; Nathan & Muller-Landau 2000), and species interactions (Simberloff & Von Holle 1999;

Callaway *et al.* 2004). Further research that directly compares transient dynamics of invasive and non-invasive species and relates transient dynamics to other important biological correlates of invasiveness will continue to shed important light on the role of stage structure in species invasions.

Acknowledgements

Data accessibility

Matrix population models: COMPADRE Plant Matrix Database (www.compadre-db.org). Descriptions of species (with associated life-history covariates) used in these analyses are listed in Table S1. R scripts: included in Appendix S1.

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Supporting Information

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

Table S1. List of species used in analyses and associated demographic/life history/citation information.

Table S2. Population viability model selection results for metrics of transient dynamics.

Table S3. Final population viability model selection results.

Appendix S1. R scripts used to simulate species introductions and calculate population viability.

Appendix S2. Correlation plots amongst eight metrics of transient dynamics following introductions of seeds.