J. Math. Biol. (2018) 77:1943–1968
https://doi.org/10.1007/s00285-018-1232-z

Mathematical Biology

Adaptive correlations between seed size and germination time

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Received: 19 December 2016 / Revised: 28 March 2018 / Published online: 20 April 2018

Abstract We present a model for the coevolution of seed size and germination time within a season when both affect the ability of the seedlings to compete for space. We show that even in the absence of a morphological or physiological constraint between the two traits, a correlation between seed size and germination time is nevertheless likely to evolve. This raises the more general question to what extent a correlation between any two traits should be considered as an a priori constraint or as an evolved means (or "instrument") to actually implement a beneficial combination of traits. We derive sufficient conditions for the existence of a positive or a negative correlation. We develop a toy model for seed and seedling survival and seedling growth and use this to illustrate in practice how to determine correlations between seed size and germination time.

Keywords Plant evolution · Adaptive syndrome · Game theory

Mathematics Subject Classification 91A22 · 92B05

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1 Introduction

Seed size and germination time are two potentially important determinants of plant establishment. Large seeds tend to produce larger and more vigorous seedlings than small seeds. Likewise, early emergence gives a seedling a competitive advantage by giving it a head start relative to seedlings that emerge later. These advantages, however, are offset by a lower per capita seed number for plants producing large seeds as well as a possibly higher per capita mortality among large seeds due to seed predators. Likewise, early germination exposes the seedling to a possibly higher risk of dying due to night frost early in the season for fast germinating seeds (see, e.g., Grubb 1977; Rees 1996; Coomes and Grubb 2003; Verdu and Traveset 2005).

Previous models have shown that the trade-off between seed size and seed number can promote the evolution of seed size variation both within and between individual plants using the same germination sites if the competitive advantage of bigger seeds is sufficiently large (Geritz 1995; Rees and Westoby 1997; Geritz et al. 1999). Differences in germination time can have similar results. In this paper we formulate a model to study the selective interaction between seed size and germination time.

If both seed size and germination time affect seedling competitive ability, it is not a priori clear how their combined effect determines the evolution of either or both. We show that even if seed size and germination time can be varied independently (i.e., if there are no physiological constraints between the two), a correlation between the two traits is nevertheless likely to evolve. This result raises the more general question whether or when a correlation between any two traits should be interpreted as a constraining factor limiting the evolution of the traits involved, or as a higher-level attribute that was selected for and evolved in order to enable an individual to actually implement an evolutionarily advantageous combination of traits. Our results not only show that the latter is possible, but we also provide a generalizable method for how such can be demonstrated in a model.

Empirical studies show that seed size and germination time within a season can be negatively correlated (Simons and Johnston 2000; Gomez 2004; Tíscar and Lucas 2010; Hojjat 2011), positively correlated (Souza and Fagundes 2014), uncorrelated (Larson 1963; Bretanolle et al. 1995; Vaughton and Ramsey 1998), or correlated in a non-monotonic way (Chacon et al. 1998). Our general model is capable of producing any type of correlation as an evolutionary outcome.

This paper is about a general idea of evolved correlations as opposed to evolution under constraints, the possible mechanisms involved (e.g., the existence of competitive ranks, see Sect. 2) and a practical method to actually calculate evolved correlations [see Sect. 3 and particularly expression (3.13)]. We also present concrete examples to illustrate the general framework, but the purpose of these models is merely to illustrate the general idea and method and emphatically not to explain specific correlations found in nature. Although the examples do allow us to relate the sign of correlations to the specific model assumptions, the models are not built with any particular species in mind.

The structure of the paper is as follows: Sect. 2 defines the concepts of seed type, strategy, fitness and competitive rank as used in this paper. Section 3 gives a general characterization of an uninvadable strategy as a probability distribution over different seed types with special emphasis on the support of the distribution and frequency-independent effects of seed type on plant fitness. Section 4 illustrates how the results of Sect. 3 can be applied to a concrete model. Section 5 gives a further general characterization of an uninvadable strategy but now with an emphasis on the actual probability mass distribution and frequency-dependent effects of seed type. Section 6 revisits the example of Sect. 4 and shows how the general results of Sect. 5 can be applied in a concrete model. In Sect. 7 we discuss our results in a wider context.

2 Strategy, fitness and competitive rank

A seed is characterized by its type $\omega := (m, t)$ where m is seed size and t germination time. Seed size m takes values in $[0, M]$, and germination time t takes values in $[0, T]$. The set of all possible seed types is thus the rectangle $\Omega := [0, M] \times [0, T]$, which we view as a subset of $\mathbf{R}^2$ equipped with the Euclidian topology. While Ω is fixed and given, there are no a priori restrictions on seed type in the interior of Ω. The seed setting strategy of a plant is a Borel probability measure π on Ω such that for every Borel set $E \subset \Omega$, $\pi(E)$ is the expected proportion of resources allocated to the production of seeds of types $\omega \in E$. We emphasize that $\pi(E)$ is generally not the same as the fraction of seeds of types $\omega \in E$, because different seed types may have different production costs and therefore can be produced in different numbers even if the amount of allocated resources is the same. In particular, the Dirac measure δ_ω is a strategy where the plant produces seeds of one type ω only (i.e., all resources are spent producing one seed type). Such a strategy is called a pure strategy. A strategy corresponding to the production of multiple seed types is called a mixed strategy.

Given a population model, a strategy is called viable if it permits a stable positive equilibrium. We refer to the population at the equilibrium as the resident population. The fitness of a strategy is the expected lifetime number of offspring produced by a single plant with that strategy. The number of offspring is calculated over one full lifecycle from the adult plant via seed production, seed dispersal and seed and seedling survival to the next generation of adult plants. The fitness of a resident strategy is necessarily equal to one.

Let $R_\pi(\omega)$ be the expected lifetime number of offspring of a plant with pure strategy δ_ω in a resident population of strategy π. The fitness of a plant with strategy $\tilde{\pi}$ (pure or mixed) in a resident population of strategy π then is

$$W_\pi(\tilde{\pi}) := \int_\Omega R_\pi(\omega) \mathrm{d}\tilde{\pi}(\omega). \tag{2.1}$$

In particular,

$$W_\pi(\pi) = 1 \tag{2.2}$$

for every viable strategy π. Next, let

$$U_\pi(\omega) := \begin{cases} \dfrac{R_\pi(\omega)}{R_0(\omega)} & \text{if } R_0(\omega) > 0 \\ 0 & \text{if } R_0(\omega) = 0 \end{cases} \tag{2.3}$$

where $R_0(\omega) > 0$ is the expected lifetime number offspring of a plant with strategy δ_ω in a competition-free environment (i.e., without a resident population) also called the basic reproduction number (Diekmann et al. 1998, 2003). Equation (2.1) can be rewritten as

$$W_\pi(\tilde{\pi}) = \int_\Omega R_0(\omega)U_\pi(\omega)\mathrm{d}\tilde{\pi}(\omega). \tag{2.4}$$

The introduction of the function $U_\pi(\omega)$ enables us to formally separate density-dependent effects of seed type on survival and fecundity from density-independent effects: all density-dependent effects are contained in $U_\pi(\omega)$, while $R_0(\omega)$ involves only density-independent effects. Formally this approach is fully general, but it may not always be clear how to explicitly express the separation in terms of specific concrete ecological processes.

Density-dependence may reduce fitness ("negative density-dependence", e.g., due to seed predation, seedling competition, herbivory and fungal infection), but it may also increase fitness ("positive density-dependence", e.g., due to beneficial effects of crowding on the micro-environment including the soil and the air quality). In this paper we only consider negative density-dependence, i.e., we assume that $R_\pi(\omega) \leq R_0(\omega)$ so that

$$0 \leq U_\pi(\omega) \leq 1 \tag{2.5}$$

for every π and every ω.

As a concrete example, in Sects. 4 and 6 we consider an annual plant species without overlapping generations and divide the season into three consecutive phases: a pre-competitive phase of seed and seedling survival and seedling growth, a competitive phase during which seedlings compete for space (i.e., sites), and a post-competitive reproductive phase. In the example, $U_\pi(\omega)$ can be interpreted as the probability that a seedling of type ω survives the competitive phase given that it survives the pre-competitive phase. However, this interpretation as a survival probability need not apply generally, i.e., outside of the example.

The dynamics of an initially rare mutant strategy $\tilde{\pi}$ in a resident population of plants with strategy π is modelled as a linear stochastic branching process (see, e.g., Haccou et al. 2005). In the supercritical case $W_\pi(\tilde{\pi}) > 1$ the mutant has a positive probability of invasion (i.e., non-extinction), while in the critical and subcritical case $W_\pi(\tilde{\pi}) \leq 1$ the mutant goes extinct with probability one. Our aim is to find an uninvadable strategy, i.e., a resident strategy that cannot be invaded by any initially rare mutant strategy.

Definition 2.1 A viable strategy π^* is uninvadable if $W_{\pi^*}(\pi) \leq 1$ for every strategy π.

Technically, this notion of an uninvadable strategy is identical to the symmetric Nash equilibrium (see, e.g., Fudenberg and Tirole 1991, p. 11; Osborne 2004, p. 52). Conceptually, however, it is more related to the evolutionarily stable strategy (ESS) of Maynard Smith and Price (1973), but there is a difference: we do not require the "second ESS condition" (Maynard Smith 1982, p. 14), which deals with the critical case $W_{\pi^*}(\tilde{\pi}) = 1$. This is a consequence of different models for the invasion dynamics of the mutant: either as a stochastic branching process assuming a finite initial number of mutant individuals (as we do here), or as a deterministic process assuming infinitely many mutants at a positive but arbitrarily small initial population density. In the former approach (which we use here) the critical case $W_{\pi^*}(\tilde{\pi}) = 1$ is non-invading, whereas the latter approach requires an additional condition (the "second ESS condition") to resolve the critical case.

After germination, seedlings may have different competitive abilities depending on their relative size, which in turn depends on seed type. We assume that each seed type can be assigned a competitive rank.

Definition 2.2 A competitive rank function is a function $r : \Omega \to \mathbf{R}$ such that $r(\omega_1) \leq r(\omega_2) \iff U_\pi(\omega_1) \leq U_\pi(\omega_2)$ for every resident strategy π. The number $r(\omega)$ is called the competitive rank of ω.

Note that a competitive rank function r induces a linear preordering $\preceq$ on Ω through the definition $\omega_1 \preceq \omega_2$ if $r(\omega_1) \leq r(\omega_2)$. Recall that $\preceq$ is a linear preordering if for every $\omega_1, \omega_2, \omega_3 \in \Omega$ either $\omega_1 \preceq \omega_2$ or $\omega_2 \preceq \omega_1$, and $\omega_1 \preceq \omega_2$, $\omega_2 \preceq \omega_3 \Longrightarrow \omega_1 \preceq \omega_3$. If we identify two seed types ω_1 and ω_2 if and only if $r(\omega_1) = r(\omega_2)$, then the preordering becomes a linear ordering on the set of equivalence classes.

A seed type with a given competitive rank produces seedlings with a higher probability of surviving competition than all other seed types with a lower competitive rank, independently of the resident's strategy. If seedlings from larger seeds as well as seedlings that emerge earlier than others have a competitive advantage as suggested in the introduction, then we must assume that $r(\omega)$ with $\omega = (m, t)$ increases with m and decreases with t. The concrete example worked out in Sects. 4 and 6 satisfies this assumption. The general theory developed in Sects. 3 and 5, however, does not need it and does not use it.

3 Properties of an uninvadable strategy

If π^* is uninvadable in the sense of Definition 2.1, then π^* is a Nash equilibrium. We can therefore use definitions and results from game theory. In particular, π^* is uninvadable if and only if $W_{\pi^*}(\delta_\omega) \leq W_{\pi^*}(\pi^*)$ for every $\omega \in \Omega$ (see, e.g., Osborne 2004, pp. 142–143). Moreover, if π^* is uninvadable, then $W_{\pi^*}(\delta_\omega) = W_{\pi^*}(\pi^*)$ π^*-almost everywhere on Ω. The latter statement is also known as the Bishop-Cannings theorem (Bishop and Cannings 1978). In the following proposition we formulate this in terms of U_π and R_0.

Proposition 3.1 *A strategy π^* is uninvadable if and only if*

$$U_{\pi^*}(\omega)R_0(\omega) \leq 1 \quad \textit{for every } \omega \in \Omega. \tag{3.1}$$

Moreover, if π^* is uninvadable, then

$$U_{\pi^*}(\omega)R_0(\omega) = 1 \quad \textit{for } \pi^*\textit{-almost every } \omega \in \Omega. \tag{3.2}$$

Proof If (3.1) is true, then from (2.4) follows immediately that $W_{\pi^*}(\pi) \leq 1$ for all π, and so π^* is uninvadable. Conversely, if there exists an $\omega_0 \in \Omega$ such that (3.1) does not hold for $\omega = \omega_0$, then $W_{\pi^*}(\pi) > 1$ for $\pi = \delta_{\omega_0}$, and so π^* is not uninvadable.

Next, suppose that π^* is uninvadable and, to reach a contradiction, suppose that there exists a set $E \subset \Omega$ with $\pi^*(E) > 0$ and $U_{\pi^*}(\omega)R_0(\omega) < 1$ for $\omega \in E$ and $U_{\pi^*}(\omega)R_0(\omega) = 1$ for $\omega \in \Omega\backslash E$. Then, by (2.4) and (2.2),

$$\begin{aligned} 1 = W_{\pi^*}(\pi^*) &= \int_E U_{\pi^*}(\omega)R_0(\omega)\mathrm{d}\pi^*(\omega) + \int_{\Omega\backslash E} \mathrm{d}\pi^*(\omega) \\ &< \pi^*(E) + \pi^*(\Omega\backslash E) = \pi^*(\Omega) = 1, \end{aligned} \tag{3.3}$$

which is a contradiction. □

Note that an uninvadable strategy π^* precludes the existence of an $\omega \in \Omega$ such that $U_{\pi^*}(\omega)R_0(\omega) > 1$. Moreover, π^* produces only seed types ω for which $U_{\pi^*}(\omega)R_0(\omega) = 1$. The support of π^* (i.e., the set of all $\omega \in \Omega$ for which $\pi^*(V) > 0$ for every neighborhood V of ω) may contain seed types for which $U_{\pi^*}(\omega)R_0(\omega) < 1$, but the set of all such seed types together has a π^*-measure equal to zero. This means that no resources at all are allocated to the production of such seed types.

The focus of the present section is on the support of an uninvadable strategy in terms of the functions r and R_0, both of which represent frequency-independent effects of seed type on plant fitness. The probability mass distribution over the support is dealt with in Sect. 5 and involves also the function U_π, which represents the frequency-dependent effects of seed size.

While Proposition 3.1 gives a full characterization of an uninvadable strategy π^* in terms of R_0 and U_{π^*}, the next proposition gives a characterization in terms of R_0 and the competitive rank r.

Proposition 3.2 *If π^* is uninvadable, then for π^*-almost every $\omega \in \Omega$*

$$R_0(\omega) \geq 1, \tag{3.4}$$

$$R_0(\omega) = \sup\{R_0(\upsilon) : \upsilon \in \Omega, \quad r(\upsilon) \geq r(\omega)\} \tag{3.5}$$

$$r(\omega) = \sup\{r(\upsilon) : \upsilon \in \Omega, \quad R_0(\upsilon) \geq R_0(\omega)\}. \tag{3.6}$$

Proof Suppose that π^* is uninvadable. Because of (3.2) in Proposition 3.1, it is sufficient to show that (3.4)–(3.6) hold for every $\omega \in \Omega$ with $U_{\pi^*}(\omega)R_0(\omega) = 1$.

Suppose $U_{\pi^*}(\omega)R_0(\omega) = 1$. Then (3.4) follows from (2.5).

Suppose that there exists an $\omega \in \Omega$ with $U_{\pi^*}(\omega)R_0(\omega) = 1$ for which (3.5) does not hold, i.e., for which there exists an $\upsilon \in \Omega$ such that $r(\upsilon) \geq r(\omega)$ and yet $R_0(\upsilon) > R_0(\omega)$. From the definition of the competitive rank it then follows that $U_{\pi^*}(\upsilon) \geq U_{\pi^*}(\omega)$. Hence, $U_{\pi^*}(\upsilon)R_0(\upsilon) > U_{\pi^*}(\omega)R_0(\omega) = 1$, which contradicts (3.1) in Proposition 3.1 and thus proves that $R_0(\omega)$ is an upper bound of $\{R_0(\upsilon) : \upsilon \in \Omega,\ r(\upsilon) \geq r(\omega)\}$, and it is obviously the least upper bound.

The proof of (3.6) is similar but with the roles of R_0 and r reversed. □

Condition (3.4) is necessary for π^* to be a viable strategy. The expressions (3.5) and (3.6) mean that an uninvadable strategy π^* produces only seeds of types that simultaneously maximize R_0 over the set of types with a greater r as well as maximize r over the set of types with a greater R_0.

Corollary 3.3 *If π^* is uninvadable, then for π^*-almost every $\omega_1, \omega_2 \in \Omega$*

$$r(\omega_1) \geq r(\omega_2) \Longleftrightarrow R_0(\omega_1) \leq R_0(\omega_2). \tag{3.7}$$

Proof By (3.5) in Proposition 3.2 we have $r(\upsilon) \geq r(\omega_2) \Longrightarrow R_0(\omega_2) \geq R_0(\upsilon)$ for π^*-almost every $\omega_2 \in \Omega$ and arbitrary $\upsilon \in \Omega$. With $\upsilon = \omega_1$, we recover the "$\Longrightarrow$" of (3.7).

Likewise, by (3.6) in Proposition 3.2 we have $R_0(\upsilon) \geq R_0(\omega_1) \Longrightarrow r(\omega_1) \geq r(\upsilon)$ for π^*-almost every $\omega_1 \in \Omega$ and arbitrary $\upsilon \in \Omega$. Taking $\upsilon = \omega_2$, we recover the "$\Longleftarrow$" of (3.7). □

Corollary 3.3 means that among the seed types actually being produced by an uninvadable strategy π^*, the offspring number (R_0) and the offspring competitive rank (r) are traded-off against one another, i.e., one seed type cannot be superior to another in terms of both offspring number and competitive rank at the same time. This is intuitively appealing, because reallocation of resources from one seed type to another that is superior in both aspects obviously would increase plant fitness and hence enable invasion, and π^* would not be uninvadable, which is a contradiction.

As R_0 and r are functions of seed type only, the characterizations of π^* in Proposition 3.2 and Corollary 3.3 are necessarily incomplete: they only involve frequency-independent (i.e., π^*-independent) consequences of seed type, and no information about the actual mass-distribution of π^* is inferred. The characterization in purely frequency-independent terms is an insight in itself, but there is a further advantage as well because no specific assumptions about U_{π^*} are being used other than that U_{π^*} takes values between zero and one. To show how such incomplete characterization can be useful, we define the set

$$\Omega_0 := \{\omega \in \Omega : \omega \text{ satisfies conditions (3.4)–(3.6)}\}. \tag{3.8}$$

With this definition it is obvious that the equivalence (3.7) holds for all $\omega_1, \omega_2 \in \Omega_0$.

Proposition 3.2 implies that if π^* is uninvadable, then π^*-almost every $\omega \in \Omega$ is an element of Ω_0. The following proposition goes one step further and states that every ω in the support of π^* is an element of the closure of Ω_0.

Proposition 3.4 *The support of an uninvadable strategy π^* is a subset of the closure of Ω_0.*

Proof Let ω be an element of the support of π^*. By the definition of the support, every neighborhood of ω has a positive π^*-measure. Hence, by Proposition 3.2, every neighborhood of ω has at least one point in Ω_0, and so $\omega \in \overline{\Omega}_0$. □

The existence and the sign of any correlation between seed size and germination time is in the first place a property of the support of π^* rather than the exact distribution of probability mass over the support. Although Ω_0 is not the support of π^*, its closure contains the support, and so we can learn about what kind of correlations between seed size and germination time are possible and which are not, by studying the geometry of Ω_0.

Therefore, from now on our focus shifts from the study of π^* to the study of Ω_0. To ensure that Ω_0 is not empty, and so to avoid trivialities, we always assume that there exists at least one $\omega \in \Omega$ for which $R_0(\omega) \geq 1$. If r and R_0 are known, then Ω_0 can be constructed graphically using its definition. This is illustrated in Fig. 1 for hypothetical but continuous r and R_0 using the level contours of both functions. In the special case where r has a plateau, i.e., there exists an open set $D \subset \Omega$ on which r is constant (not illustrated in the figure), then $\omega \in \overline{D} \cap \Omega_0$ maximizes R_0 on the closure $\overline{D}$ of the plateau. On the other hand, if R_0 has a plateau, then r is maximized. If r and R_0 have overlapping plateaus, then all seed types in D are selectively neutral to one another.

If r and R_0 are smooth functions, then Ω_0 can be characterized in terms of the derivatives of R_0 and r, which gives a tool to study seed size and germination time using ordinary calculus. Here and in the sequel, ∇ denotes the gradient of a real-valued function of two variables. In particular, $\det(\nabla r, \nabla R_0) = \frac{\partial r}{\partial m}\frac{\partial R_0}{\partial t} - \frac{\partial R_0}{\partial m}\frac{\partial r}{\partial t}$.

Proposition 3.5 *Let R_0 and r be twice continuously differentiable in the interior of Ω. Then, for every $\omega_0 \in \Omega_0 \cap \operatorname{int}\Omega$*

$$\nabla r \cdot \nabla R_0 \leq 0, \tag{3.9}$$

$$\det(\nabla r, \nabla R_0) = 0, \tag{3.10}$$

$$\begin{pmatrix} -\partial r/\partial t \\ \partial r/\partial m \end{pmatrix} \cdot \nabla \det(\nabla r, \nabla R_0) \leq 0. \tag{3.11}$$

The proof of Proposition 3.5 is given in the Appendix; here we only give an interpretation. First note that the set Ω of all possible seed types is by its definition compact, and since r and R_0 are now assumed to be continuous functions, the supremum in (3.5) and (3.6) in the definition of Ω_0 can be replaced by a maximum. Thus, $\omega_0 \in \Omega_0 \cap \operatorname{int}\Omega$ maximizes R_0 over the set $\{\upsilon \in \Omega : r(\upsilon) \geq r(\omega_0)\}$ and at the same time maximizes r over the set $\{\upsilon \in \Omega : R_0(\upsilon) \geq R_0(\omega_0)\}$. In both cases the maximum lies on the boundary of these sets, and (3.9) and (3.10) in Proposition 3.5 are necessary conditions for a local extremum located on the boundary, and (3.11) is a necessary condition for the extremum to be a local maximum.

In geometric terms (3.9) means that, for every $\omega_0 \in \Omega_0 \cap \operatorname{int}\Omega$, the angle between the gradient vectors $\nabla r(\omega_0)$ and $\nabla R_0(\omega_0)$ is greater than 90°, and condition (3.10) means that the gradient vectors are linear dependent, so that the angle is either zero or 180°. The two conditions together thus imply that $\nabla r(\omega_0)$ and $\nabla R_0(\omega_0)$ point in exactly opposite directions. The tangent vectors of the level contours of the functions r and R_0 at ω_0 are orthogonal to $\nabla r(\omega_0)$ and $\nabla R_0(\omega_0)$ and hence parallel to each other (Fig.1d).

Condition (3.11) compares the curvatures of the level contours of the functions r and R_0 at ω_0. This may be not immediately obvious, but it is shown in the Appendix after the proof of Proposition 3.5. If the orientation of the level contours (i.e., the direction of moving along a contour) is defined by the vector obtained by the counter-clockwise rotation of $\nabla r(\omega_0)$ over 90° and, moreover, if the curvature of a level contour is defined to be positive if the (now oriented) contour turns counter-clockwise and negative if it turns the other way, then (3.11) means that at ω_0 the curvature of the level contour of r

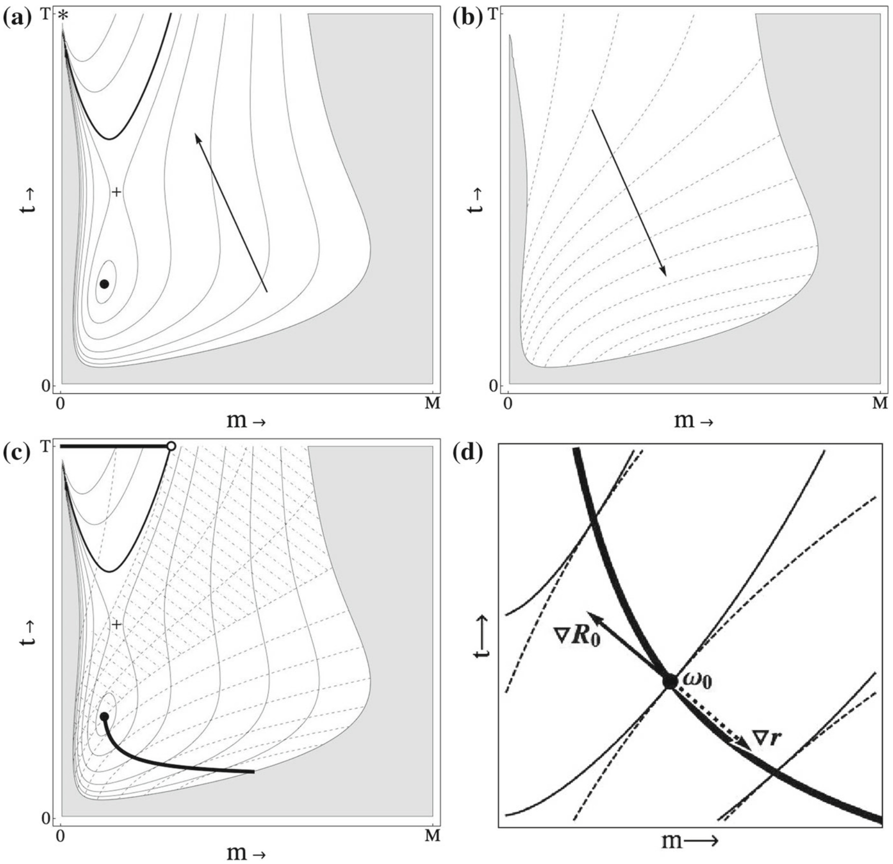

Fig. 1 Graphical construction of the set Ω_0 for hypothetical R_0 and r. The subset of Ω where $R_0(\omega) \geq 1$ is colored white. Panel **a** shows the contour lines of the function R_0 with the arrow pointing towards higher values. The star in the upper-left indicates the global maximum of R_0, the dot a local maximum, and the cross a saddle point. The thick contour line in the upper left of the panel coincides with the value of R_0 at the local maximum. Panel **b** shows the contour lines of the function r with the arrow pointing towards higher values. Only contour lines inside the white subset defined by $R_0(\omega) \geq 1$ are shown. Panel **c** is the superposition of panels **a** and **b** with some extra features added. The additional thick lines indicate the set Ω_0. It can be seen that every $\omega \in \Omega_0$ maximizes R_0 over the set of seed types with a higher or equal competitive rank r. Similarly, every $\omega \in \Omega_0$ maximizes r over the set of seed types with a higher or equal R_0. The open circle at the top of the panel indicates a point that maximizes R_0 but not r, i.e., it satisfies conditions (3.4) and (3.5) but not (3.6) and thus does not belong to Ω_0 (but does belong to the closure of Ω_0). The shaded subset inside the white subset coincides with values of r that do not occur in Ω_0. Panel **d** shows a detail of panel **c**, illustrating that the contours of continuously differentiable R_0 and r at $\omega_0 \in \Omega_0$ in the interior of Ω are tangent to one another, and that the gradients of R_0 and r at ω_0 point in exactly opposite directions (this follows from Proposition 3.5)

is smaller than the curvature of the level contour of R_0 (Fig. 2a). If the curvatures were ordered in the opposite way, then ω_0 would correspond to a local minimum (rather than maximum) of the functions r and R_0 over the sets $\{\upsilon \in \Omega : R_0(\upsilon) \geq R_0(\omega_0)\}$ and $\{\upsilon \in \Omega : r(\upsilon) \geq r(\omega_0)\}$, respectively (Fig. 2b).

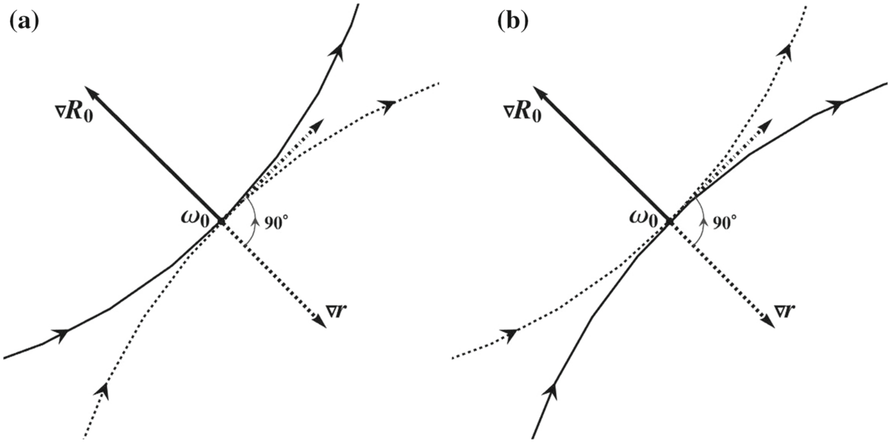

Fig. 2 On the geometric interpretation of Proposition 3.5 at every $\omega_0 \in \Omega_0 \cap \operatorname{int} \Omega$, the gradient vectors ∇r and ∇R_0 point in exactly opposite directions and are orthogonal to the tangents of the level contours of the function R_0 (solid curve) and the function r (dashed curve). Both level curves are oriented by the (dot-dashed) vector that is obtained by rotating ∇r over 90° counter-clockwise. In (a) the level contour of R_0 has a greater curvature than the level contour of r, and ω_0 maximizes r and R_0 over the sets $\{\upsilon \in \Omega : R_0(\upsilon) \geq R_0(\omega_0)\}$ and $\{\upsilon \in \Omega : r(\upsilon) \geq r(\omega_0)\}$, respectively. In (b) the level contour of R_0 has a smaller curvature than the level contour of r, and ω_0 minimized r and R_0 over the respective sets

Condition (3.10) is the most important of the three conditions in Proposition 3.5, because it implicitly defines Ω_0 in the interior of Ω as a curve and gives a potential relation between seed size m and germination time t. In particular, if the tangent to Ω_0 (if such a tangent exists) has a positive slope dt/dm, then a potential local correlation will be positive, but if the tangent has a negative slope, then a potential local correlation will be negative. The following corollary gives a condition for the existence of the tangent as well as an explicit expression of the tangent vector.

Corollary 3.6 *Let R_0 and r be twice continuously differentiable in the interior of Ω. Then, for every $\omega_0 \in \Omega_0 \cap \operatorname{int} \Omega$ with*

$$\nabla \det(\nabla r, \nabla R_0) \neq 0, \tag{3.12}$$

Ω_0 is locally the image of a continuously differential curve with tangent vector

$$u = (u_1, u_2) = \left(-\frac{\partial}{\partial t} \det(\nabla r, \nabla R_0), \frac{\partial}{\partial m} \det(\nabla r, \nabla R_0)\right)^\top. \tag{3.13}$$

Proof Condition (3.10) in Proposition 3.5 means that Ω_0 coincides with the zero-level contour line of the function $\det(\nabla r, \nabla R_0)$. This contour has a well defined tangent that is orthogonal to $\nabla \det(\nabla r, \nabla R_0)$, provided the latter is not zero. □

Therefore, the sign of a potential local correlation between seed size and germination time is positive if the scalar components u_1 and u_2 of u in (3.13) have the same sign and negative if u_1 and u_2 have opposite signs. Furthermore, if u_1 and u_2 do not change sign, then the sign of a potential correlation is the same everywhere in the interior of Ω. However, if $|u_1 - u_2|$ is large, then the tangent will be almost horizontal or vertical, and so either m or t is almost constant.

4 Example

In this section we present a concrete model as an example to show how the general results of the previous section can be applied in practice to a particular case. We emphasize that, for the purpose of illustration, the model is intentionally kept simple, and the analysis is not meant to be comprehensive.

To get results that can be related to seed and seedling survival and seedling growth as functions of seed size and germination time, we need a more specific model. To that end we consider an annual plant species without overlapping generations and divide the season into three consecutive phases: a pre-competitive phase of seed and seedling survival and seedling growth, a short but intense competitive phase during which seedlings compete for space while seedling growth is negligible, and a post-competitive reproductive phase.

The pre-competitive phase coincides with the time interval $[0, T]$. We assume that the probability that a seed of type $\omega = (m, t)$ and the ensuing seedling survive till time T is

$$L(\omega) := e^{-t\,\mu(m) - \int_t^T \nu(\tau)\mathrm{d}\tau}. \tag{4.1}$$

Here $\mu(m)$ and $\nu(\tau)$ denote the seed and seedling mortality rates, respectively, at time $\tau \in [0, T]$. We further assume that a seedling that survives till the end of the pre-competitive phase has the size

$$S(\omega) := \alpha\, m\, e^{\int_t^T \lambda(\tau)\mathrm{d}\tau}, \tag{4.2}$$

where $\lambda(\tau)$ is the seedling's growth rate (per mass) at time $\tau \in [0, T]$, and where the initial seedling size is proportional to seed size with constant of proportionality $\alpha > 0$. We also assume that larger seedlings are competitively superior to smaller ones, so that we can equate the competitive rank with seedling size at time T, i.e.,

$$r(\omega) = S(\omega). \tag{4.3}$$

This model of seedling growth and competitive rank incorporates the notion of large seed size and early germination being advantageous when it comes to seedling competition.

We assume that $\lambda, \nu\colon (0, T) \to \mathbf{R}_+$ and $\mu\colon (0, M) \to \mathbf{R}_+$ are twice continuously differentiable functions. For R_0 we consider two different models. In the first model the per capita amount of resources available for seed production is proportional the size of the seedling at the end of the pre-competitive phase, the idea being that after competition all plants continue to grow at the same exponential rate:

$$R_0(\omega) := L(\omega)\,\frac{\beta S(\omega)}{m + \gamma}. \tag{4.4}$$

Here $\beta > 0$ is the constant of proportionality relating resources available for seed production to seedling size at the end of the pre-competitive phase, and $\gamma > 0$ is the production cost per seed. We refer to this model as the "proportional resources".

In the second model the per capita amount of resources is fixed, the idea being that plant growth and the final size are limited by the locally available resources:

$$R_0(\omega) := L(\omega)\,\frac{\beta}{m+\gamma}. \tag{4.5}$$

Now β is the fixed amount of resources available for seed production, independently of seedling size. We refer to this model as the "fixed resources".

Both models have implemented a trade-off between seed size and seed number, and both models account for seed type affecting survival and establishment of seeds and seedlings. In the first model, however, seed type affects also the fecundity of established plants by affecting the amount of available resources, while in the second model seed type has no effects beyond the competitive phase.

The following two propositions give necessary conditions for (m, t) to be a point of Ω_0 in the interior of Ω:

Proposition 4.1 (Proportional resources) *Let R_0 be defined by (4.4). Then, for every $(m, t) \in \Omega_0 \cap \operatorname{int} \Omega$,*

$$\nu(t) - \mu(m) \geq \lambda(t) > 0, \tag{4.6}$$

$$\mu'(m) \geq \frac{\gamma}{t\,m\,(m+\gamma)} > 0. \tag{4.7}$$

Proposition 4.2 (Fixed resources) *Let R_0 be defined by (4.5). Then, for every $(m, t) \in \Omega_0 \cap \operatorname{int} \Omega$,*

$$\nu(t) - \mu(m) \geq 0, \tag{4.8}$$

$$\mu'(m) \geq \frac{-1}{t\,(m+\gamma)} < 0. \tag{4.9}$$

The proofs are given in the Appendix. Here we only comment on the meaning and the consequences of the propositions. Note that at every point of Ω_0 in the interior of Ω and hence, by Proposition 3.4, at every point of the support of an uninvadable strategy π^* in the interior of Ω, the following is required: Firstly, the seed has a lower mortality rate than the seedling. This is true for both models of R_0. However, in the case of proportional resources, the required difference in mortality rates increases with the seedling growth rate. Secondly, with proportional resources seed mortality is locally a strictly increasing function of seed size, and more strongly so if seed size is small or germination time is short (Fig. 3a). With fixed resources, however, seed mortality may be increasing or decreasing (Fig. 3b, c).

If the conditions are not satisfied at a given point in the interior of Ω, then that point is not in Ω_0 and hence also not in the support of π^*. Thus, if seed mortality is greater than seedling mortality for all seed types, which violates both (4.6) and (4.8),

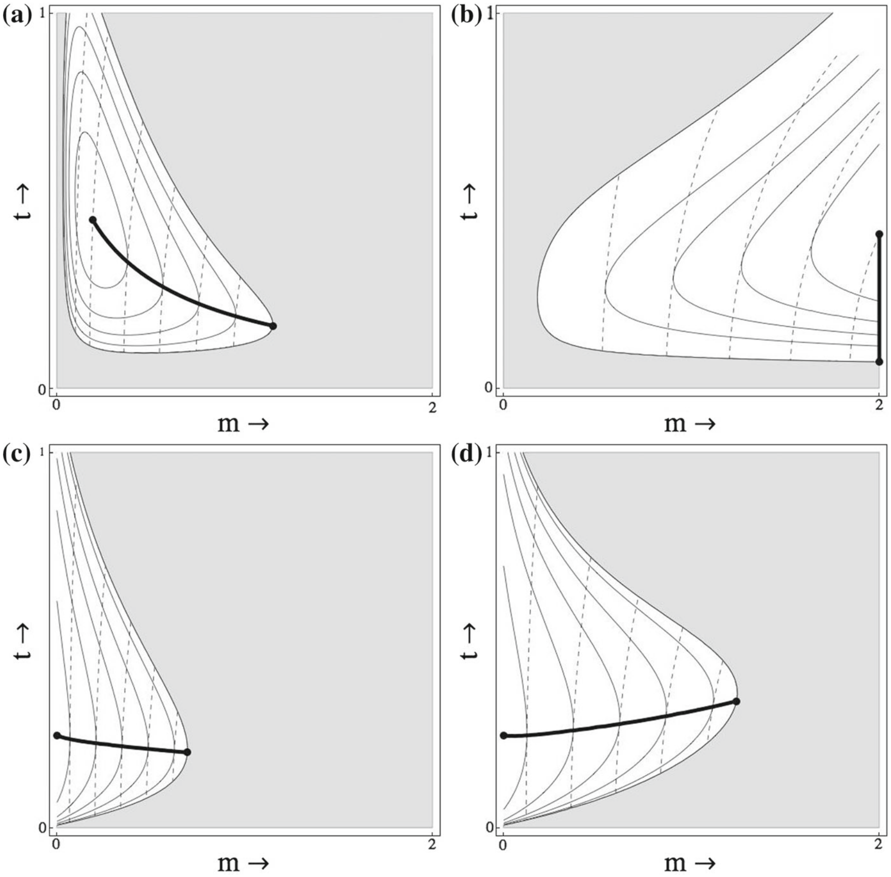

Fig. 3 Examples of Ω_0. The subset of Ω where $R_0(\omega) \geq 1$ is colored white. The contour lines of R_0 are shown with a thin, solid line. The contour lines of r are shown with a dashed line. The thick lines indicate the set Ω_0. In the upper row R_0 is given by (4.4) where the per capita resources are proportional to plant size. In the lower row R_0 is given by (4.5) where the per capita resources are fixed. In all four panels λ is an increasing function and ν a decreasing function, but μ is an increasing function in the left column and a decreasing function in the right column. Specifically, we use $\lambda(t) = at$, $\mu(m) = b + cm$ and $\nu(t) = (t + d)^{-1}$ with $a = 1$, $d = .004$, $\alpha = 1$, $\beta = 1$, $\gamma = .1$, $M = 2$ and $T = 1$. Moreover, in panel **a** we have $b = 1$ and $c = 4$; in **b** $b = 4$ and $c = -1$; in **c** $b = 4$ and $c = 1$; and again in **d** $b = 4$ and $c = -1$

then the entire set Ω_0 necessarily lies on the boundary of Ω, independently of which model for R_0 we use. Likewise, if seed mortality is a decreasing function of seed size everywhere, which is a violation of (4.7), then Ω_0 lies on the boundary of Ω in the case of proportional resources (Fig. 3b), but not necessarily so for fixed resources (Fig. 3d).

The following proposition gives sufficient conditions that guarantee that the tangent to Ω_0 at a given point has a negative slope so that a possible correlation between seed size and germination time is locally negative:

Proposition 4.3 (Proportional resources and fixed resources) *Let* R_0 *be given by* (4.4) *or* (4.5), *and let* $(m, t) \in \Omega_0 \cap \operatorname{int} \Omega$ *be such that* $\lambda'(t) > 0$, $\mu'(t) > 0$, $\nu' < 0$, $\mu''(m) \geq 0$ *and* $\nu - \mu > \lambda$. *Then, the components of the tangent vector* (3.13) *have opposite signs, and hence the tangent to* Ω_0 *has a negative slope.*

The proof is given in the Appendix. Note that the conditions $\mu'(t) > 0$ and $\nu - \mu > \lambda$ are readily satisfied for the case of proportional resources because of Proposition 4.1, but not necessarily so for the case of fixed resources. Violation of $\mu'(t) > 0$ in the case of fixed resources can lead to a positive slope of the tangent to Ω_0 (Fig. 3d).

5 Properties of an uninvadable strategy with support in Ω_0

With Proposition 3.4 the problem of finding an uninvadable strategy π^* with support in the rectangle Ω has been reduced to the simpler problem of finding an uninvadable strategy with support in the smaller set $\overline{\Omega}_0$. Does this mean that a strategy uninvadable on Ω_0 is also uninvadable on the whole of Ω? The following proposition says that this is indeed the case.

Proposition 5.1 *For given* π, *suppose that* $U_\pi(\omega) R_0(\omega) \leq 1$ *for every* $\omega \in \Omega_0$. *Then* $U_\pi(\omega) R_0(\omega) \leq 1$ *for every* $\omega \in \Omega$ *and hence* π *is uninvadable.*

Proof To reach a contradiction, suppose that there exists an $\omega_1 \in \Omega$ such that $U_\pi(\omega_1) R_0(\omega_1) > 1$. Since $U_\pi(\omega_1) \leq 1$, necessarily $R_0(\omega_1) > 1$.

Let $\omega_2 \in \Omega$ be such that $R_0(\omega_2) = \sup\{R_0(\upsilon) \colon \upsilon \in \Omega, r(\upsilon) \geq r(\omega_1)\}$. Then, $R_0(\omega_2) \geq R_0(\omega_1) > 1$ and $r(\omega_2) \geq r(\omega_1)$ and furthermore

$$R_0(\omega_2) = \sup\{R_0(\upsilon) \colon \upsilon \in \Omega,\ r(\upsilon) \geq r(\omega_2)\}. \tag{5.1}$$

Now, let $\omega_3 \in \Omega$ be such that $r(\omega_3) = \sup\{r(\upsilon) \colon \upsilon \in \Omega, R_0(\upsilon) \geq R_0(\omega_2)\}$. Then, $r(\omega_3) \geq r(\omega_2)$ and $R_0(\omega_3) \geq R_0(\omega_2)$. On the other hand,

$$\begin{aligned} R_0(\omega_2) &= \sup\{R_0(\upsilon) \colon \upsilon \in \Omega,\ r(\upsilon) \geq r(\omega_2)\} \\ &\geq \sup\{R_0(\upsilon) \colon \upsilon \in \Omega,\ r(\upsilon) \geq r(\omega_3)\} \\ &\geq R_0(\omega_3) \geq R_0(\omega_2), \end{aligned} \tag{5.2}$$

and so the $\geq$ signs in (5.2) can be replaced by $=$ signs. Therefore,

$$R_0(\omega_3) = R_0(\omega_2) \geq R_0(\omega_1) > 1, \tag{5.3}$$

$$R_0(\omega_3) = \sup\{R_0(\upsilon) \colon \upsilon \in \Omega,\ r(\upsilon) \geq r(\omega_3)\}, \tag{5.4}$$

$$r(\omega_3) = \sup\{r(\upsilon) \colon \upsilon \in \Omega,\ R_0(\upsilon) \geq R_0(\omega_3)\}, \tag{5.5}$$

which by definition means that $\omega_3 \in \Omega_0$. Hence,

$$1 \geq U_\pi(\omega_3) R_0(\omega_3) \geq U_\pi(\omega_2) R_0(\omega_2) \geq U_\pi(\omega_1) R_0(\omega_1) > 1, \tag{5.6}$$

which is a contradiction. □

The restriction to the smaller set Ω_0 is an application of the so-called "method of elimination of dominated strategies" (see, e.g., Fudenberg and Tirole 1991, pp. 9–11; Osborne 2004, pp. 385–387).

The main idea of this section is that instead of searching directly for an uninvadable strategy on Ω_0, we first look for an uninvadable strategy over the corresponding range of competitive ranks and then translate the result back in terms of seed types. To see how this works, first note that from the definition of Ω_0 in (3.8) it is clear that the equivalence (3.7) holds for all $\omega_1, \omega_2 \in \Omega_0$, and so

$$r(\omega_1) = r(\omega_2) \Longleftrightarrow R_0(\omega_1) = R_0(\omega_2). \tag{5.7}$$

Secondly, from Definition 2.2 we have

$$r(\omega_1) = r(\omega_2) \Longleftrightarrow U_\pi(\omega_1) = U_\pi(\omega_2), \tag{5.8}$$

which in combination with (5.7) gives

$$r(\omega_1) = r(\omega_2) \Longleftrightarrow R_0(\omega_1)U_\pi(\omega_1) = R_0(\omega_2)U_\pi(\omega_2) \tag{5.9}$$

for every resident strategy π. In other words, every $\omega_1, \omega_2 \in \Omega_0$ with equal competitive ranks contribute to fitness in exactly the same way, i.e., they are selectively neutral to one another irrespectively of the resident's strategy. If we identify seed types in with the same competitive rank, then the competitive rank function r induces a linear ordering on Ω_0 (see remark under Definition 2.2). In particular, there is a one-to-one relation between equivalence classes of seed types in Ω_0 and the corresponding competitive rank. This justifies the "change of variables" from seed type (or rather, equivalence classes of seed types) to competitive rank in order to solve first the problem of finding an uninvadable strategy over the set of competitive ranks and then translate the result back in terms of seed types.

To this end define the probability measure ϑ_π on the set $r(\overline{\Omega}_0)$ by

$$\vartheta_\pi(J) = \pi(r^{-1}(J)), \tag{5.10}$$

for all Borel sets $J \subset r(\overline{\Omega}_0)$. Moreover, define $\widetilde{R}_0 : r(\overline{\Omega}_0) \to \mathbb{R}$ and $\widetilde{U}_\pi : r(\overline{\Omega}_0) \to \mathbb{R}$ by

$$\begin{aligned} \widetilde{R}_0(r(\omega)) &= R_0(\omega), \\ \widetilde{U}_\pi(r(\omega)) &= U_\pi(\omega) \end{aligned} \tag{5.11}$$

for all $\omega \in \overline{\Omega}_0$.

Proposition 5.2 *The Borel probability measure π on Ω with* $\operatorname{supp}(\pi) \subset \overline{\Omega}_0$ *is uninvadable if and only if $\widetilde{U}_\pi(\rho)\widetilde{R}_0(\rho) \le 1$ for all $\rho \in r(\overline{\Omega}_0)$.*

Proof From (5.11) we have that $\widetilde{U}_\pi(r(\omega))\widetilde{R}_0(r(\omega)) = U_\pi(\omega)R_0(\omega)$. From Propositions 3.1 and 5.1 then follows that π is uninvadable if and only if $\widetilde{U}_\pi(\rho)\widetilde{R}_0(\rho) \le 1$ for all $\rho \in r(\overline{\Omega}_0)$. □

6 Example (continued)

In the example of Sect. 4 the focus was on the construction of Ω_0. The set $\overline{\Omega}_0$ contains the support of an uninvadable strategy π^*, but it is not the support itself. The actual support will depend not only on r and R_0 but also on the competition function U_π, which we have not considered yet. To specify U_π one has to make assumptions about the underlying biology and especially about the mechanism of competition. Following Geritz (1995) we make the following assumptions: seedlings compete for discrete sites. The number of seeds that land in any particular site is stochastic and follows a Poisson distribution. Each site is just large enough for the establishment of a single individual plant only. If two or more seeds end up in the same site, then seedlings will compete such that only one will become established. Competition is extremely asymmetric, i.e., the winner in a given site is always one with the highest competitive rank among all seedlings present.

Consider a resident with a seed setting strategy π with support in $\overline{\Omega}_0$, and let ϑ_π, $\widetilde{R}_0$ and $\widetilde{U}_\pi$ be defined as in (5.10)–(5.11). The plant density N, measured as the fraction of occupied sites, is equal to the fraction of sites that receive at least one seed produced in the previous year, i.e.,

$$N(t+1) = 1 - \exp\left\{-N(t)\int_{r(\overline{\Omega}_0)} \widetilde{R}_0(\theta)\mathrm{d}\vartheta_\pi(\theta)\right\}. \tag{6.1}$$

For $\int_{r(\overline{\Omega}_0)} \widetilde{R}_0(\theta)\mathrm{d}\vartheta_\pi(\theta) > 1$ there exists a unique positive and stable equilibrium N that satisfies the equation

$$N = 1 - \exp\left\{-N\int_{r(\overline{\Omega}_0)} \widetilde{R}_0(\theta)\mathrm{d}\vartheta_\pi(\theta)\right\}. \tag{6.2}$$

Let $J(\rho)$ be the subset of $r(\overline{\Omega}_0)$ containing precisely those competitive ranks that are strictly greater than ρ. The probability that a given seedling with competitive rank $\rho \in r(\overline{\Omega}_0)$ wins the competition in a random site then is

$$\begin{aligned}\widetilde{U}_\pi(\rho) &= \exp\left\{-N\int_{J(\rho)} \widetilde{R}_0(\theta)\mathrm{d}\vartheta_\pi(\theta)\right\}\left(e^{-\vartheta_\pi(\{\rho\})N}\sum_{k\geq 0}\frac{1}{k+1}\frac{(\vartheta_\pi(\{\rho\})N)^k}{k!}\right)\\ &= \exp\left\{-N\int_{J(\rho)} \widetilde{R}_0(\theta)\mathrm{d}\vartheta_\pi(\theta)\right\}\left(\frac{1-e^{-\vartheta_\pi(\{\rho\})N}}{\vartheta_\pi(\{\rho\})N}\right), \end{aligned} \tag{6.3}$$

which is the probability that a site does not contain any seedlings with a rank strictly greater than ρ times the probability of winning in a site with $k \geq 0$ competitors with exactly the same competitive rank.

Proposition 6.1 *Suppose* $\widetilde{R}_0$ *is differentiable,* r *continuous, and* $r(\overline{\Omega}_0) = [\rho_{\min}, \rho_{\max}]$ *with* $\widetilde{R}_0(\rho_{\max}) = 1$. *If* ϑ_π *is the probability measure on* $r(\overline{\Omega}_0)$ *induced by the Borel probability measure* π *on* Ω *with* $\operatorname{supp}(\pi) \subset \overline{\Omega}_0$, *and* ϑ_π *has the probability density*

$$\phi(\rho) = c \, \frac{\mathrm{d}}{\mathrm{d}\rho} \widetilde{R}_0(\rho)^{-1} \tag{6.4}$$

for all $\rho \in [\rho_{\min}, \rho_{\max}]$, *where*

$$c = \frac{\widetilde{R}_0(\rho_{\min})}{\widetilde{R}_0(\rho_{\min}) - 1} \tag{6.5}$$

is a normalization constant, then π *is uninvadable.*

Proof If ϑ_π has the probability density ϕ, then the equilibrium equation (6.2) becomes

$$N = 1 - \widetilde{R}_0(\rho_{\min})^{-cN}, \tag{6.6}$$

which is solved by

$$N = 1 - \widetilde{R}_0(\rho_{\min})^{-1}, \tag{6.7}$$

and the competition function in (6.3) simplifies to

$$\widetilde{U}_\pi(\rho) = \widetilde{R}_0(\rho)^{-1} \tag{6.8}$$

so that

$$\widetilde{U}_\pi(\rho)\widetilde{R}_0(\rho) = 1 \tag{6.9}$$

for all $\rho \in [\rho_{\min}, \rho_{\max}]$. It follows from Proposition 5.2 that π is uninvadable. $\square$

We now apply Proposition 6.1 to the examples in Sect. 4. To present the results in terms of seed types rather than competitive rank we proceed as follows. For $\omega = (m, t) \in \overline{\Omega}_0$ we have

$$\widetilde{R}_0(r(\omega)) = R_0(\omega), \tag{6.10}$$

and so the derivative of $\widetilde{R}_0$ at $r(\omega)$ is given by

$$\widetilde{R}_0'(r(\omega)) = \frac{\nabla R_0(\omega) \cdot u}{\nabla r(\omega) \cdot u}, \tag{6.11}$$

where u is the vector given in (3.13).

For ϕ we have

$$\phi(r(\omega)) = -\frac{c}{R_0(\omega)^2} \frac{\nabla R_0(\omega) \cdot u}{\nabla r(\omega) \cdot u} \tag{6.12}$$

with

$$c = \left(1 - \frac{1}{R_0^{\max}}\right)^{-1}, \tag{6.13}$$

where $R_0^{\max}$ is the maximum of R_0 over $\overline{\Omega}_0$ and it is attained where the competitive rank is at its minimum. Figure 4a, c, d show the graphs of $\phi(r(\omega))$ for the examples in Sect. 4 corresponding to Fig. 3a, c, d where Ω_0 lies almost entirely in the interior of Ω.

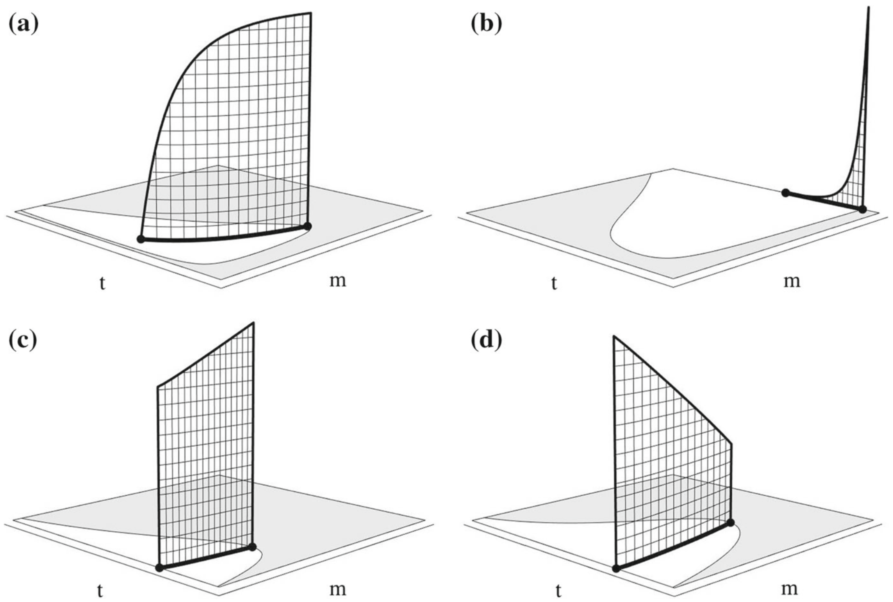

Fig. 4 Examples of $\phi(r(\omega))$ for $\omega = (m, t) \in \Omega_0$. The successive panels correspond to the examples used in Fig. 3. The origin of the graphs is in the front corner. From there germination time t runs up to the left, and seed size m runs up to the right. The scale of the vertical axis is arbitrary. For convenience of comparison, the grey and white regions correspond with those in Fig. 3

If Ω_0 is a subset of the boundary of Ω, then u is just a unit vector along the boundary. For example, in the case shown in Fig. 3b, $u = (0, -1)$ and we get

$$\widetilde{R}_0'(r(\omega)) = \frac{\partial R_0(\omega)}{\partial t} \left(\frac{\partial r(\omega)}{\partial t} \right)^{-1}. \tag{6.14}$$

Hence for ϕ we get

$$\phi(r(\omega)) = -\frac{c}{R_0(\omega)^2} \cdot \frac{\partial R_0(\omega)}{\partial t} \left(\frac{\partial r(\omega)}{\partial t} \right)^{-1} \tag{6.15}$$

where c is as in (6.13). Figure 4b shows the graph of $\phi(r(\omega))$ for the example in Sect. 4 corresponding to Fig. 3b.

7 Discussion

In this paper we formulated a model for the coevolution of seed size and (within-season) germination time when both traits affect the ability of the seedlings to compete for space. We showed that if seedlings can be assigned a competitive rank depending on seed type (i.e., seed size and germination time) such that a seedling with a higher competitive rank has a higher probability of surviving competition independently of the resident's strategy, then the support of an uninvadable strategy as a distribution over seed types is confined within a one-dimensional subset of the larger two-dimensional set of all seed types. The reason for this is that among seedlings of equal competitive rank, only the type that produces the most new seeds is evolutionarily favoured. This is an application of the "method of elimination of dominated strategies" (see, e.g., Fudenberg and Tirole 1991, pp. 9–11; Osborne 2004, pp. 385–387). As a consequence, a correlation between seed size and germination time is likely to evolve whenever there is any variation in seed types at all (Fig. 1).

The existence of a competitive rank is an assumption. If there exists a competitive rank, however, then the problem of finding an uninvadable strategy as a distribution over the two-dimensional space of all seed types is reduced to a one-dimensional subset of that space. In principle, this reduction seems possible even with higher-dimensional problems. With the reduction, the present problem becomes mathematically similar to the one considered by Geritz (1995) and Geritz et al. (1999) where the competitive rank was determined by seed size only, and where it was shown that mixed (i.e., polymorphic) strategies evolve if the competition between seedlings with different competitive ranks is sufficiently asymmetric in favour of those of a higher competitive rank.

Our model covers both between-plant and within-plant variation of seed types (or any mixture of the two) as long as the probability of encountering competitors of a given seed type depends only on the population-level distribution of seed types: in this case, it does not matter whether the mixed ESS represents a coalition of individuals all using the same mixed strategy or a coalition of individuals each of whom uses a pure strategy with their relative frequencies corresponding to the mixed strategy ESS (see Discussion in Geritz 1995).

To relate the results to seed and seedling survival and seedling growth as functions of seed size and germination time, we formulated a more specific model that is capable of producing different kinds of correlations as an evolutionary outcome (Fig.2). In particular, we found that if, during the pre-competitive phase, seed mortality rapidly increases with seed size (e.g., because of seed predators preferring larger seeds) and seedling mortality decreases with seed size (e.g., due to seedlings from larger seeds being more robust) and seedling growth rate increases with time (e.g., because of increasing temperatures and generally improving whether conditions), then evolution favours early germination of large seeds and later germination of small seeds (see Proposition 4.3). As these conditions occur quite naturally (see, e.g., Grubb 1977; Coomes and Grubb 2003), a negative correlation between seed size and germination time seems to be the more likely outcome of the model under realistic assumptions.

To calculate the actual shape of an uninvadable seed type distribution (as opposed to merely its support) we considered a further specification of the model including site competition with only one surviving seedling per site, random seed dispersal with Poisson-distributed numbers of seed landings per site, and extremely asymmetric competition such that the winner in a given site is always one with the highest competitive rank among all seedlings present. The resulting evolutionary outcome is a seed type distribution with a continuous support (Fig. 3). Similar results for the evolution of seed size only were found by Geritz (1995), but results from Geritz et al. (1999) suggest that with less extreme competitive asymmetry (such that also seedlings with a lower competitive rank have a chance of winning local competition) the support crumbles into finitely many isolated points. This also follows from a more general result by Gyllenberg and Meszena (2005) on the generic impossibility of coexistence of infinitely many types. However, Haccou and Iwasa (1998) have shown that the continuous distribution in the extremely asymmetric limit can be expected to be a good approximation to the discrete distribution with strong asymmetric competition.

We used the notion of the Nash equilibrium rather than the evolutionarily stable strategy (ESS) of Maynard Smith (1982). This reflects a choice of model for the dynamics of an initially rare mutant strategy: either as a stochastic branching process assuming a finite initial number of mutant individuals (as we did here in this paper), or as a deterministic process assuming infinitely many mutants at a positive but arbitrarily small initial population density. This was not an arbitrary choice: the ESS conditions (in particular the so-called "second ESS condition" in Maynard Smith 1982, p. 14) would be difficult to verify and also difficult to interpret, because of the non-linear dependence of the invader's fitness on the resident's strategy.

Models for the coevolution of different seed characteristics (such as seed size and within season germination time as in the present model, but also possibly involving local adaptation, dormancy and dispersal; see, e.g., Brown and Venable 1986) are important for our understanding of adaptive correlations. A particularly interesting question is as to what extent an empirically observed correlation between two traits should be interpreted as a constraining factor or as a property that evolved in order to enable an individual to actually implement an evolutionarily advantageous strategy. In this paper we have shown how competition within a population may drive evolution to produce correlations between different traits. Other possible evolutionary mechanisms producing correlations could be, for example, independent adaptation of different traits to local environments in a heterogeneous landscape.

We made two assumptions that restrict the generality of our results, i.e., we assumed negative density-dependence and we assumed that there exists a competitive rank order. However, in spite of these restrictions, our method of analysis is generalizable to a wider context than the evolution of seed traits. The essential issue of our approach is the restriction of frequency-dependence to a submanifold of a higher dimensional strategy space. This directly links back to the more general question raised in the Introduction whether or when a correlation between any two traits should be interpreted as a morphological tradeoff constraining the evolution of the traits involved, or as an evolutionary outcome. Our results show that the latter is possible indeed and moreover provides a method of studying this phenomenon.

Acknowledgements We would like to thank Troy Day, Tuomas Hytönen and three anonymous reviewers for helpful comments on an earlier draft of this article. This research was funded by the Academy of Finland.

8 Appendix

8.1 Proof of Proposition 3.5

Let R_0 and r be twice continuously differentiable in the interior of Ω, and let $\omega_0 \in \Omega_0 \cap \operatorname{int} \Omega$ be such that $\nabla r(\omega_0)$ and $\nabla R_0(\omega_0)$ are both non-zero (if $\nabla r(\omega_0) = 0$ or $\nabla R_0(\omega_0) = 0$, then (3.9)–(3.11) are trivially true).

To prove (3.9), let $\varepsilon > 0$ be such that $\omega_0 + \varepsilon \nabla r(\omega_0) \in \Omega$ and

$$r(\omega_0 + \varepsilon \nabla r(\omega_0)) = r(\omega_0) + \varepsilon ||\nabla r(\omega_0)||^2 + O(\varepsilon^2) > r(\omega_0). \tag{8.1}$$

Then, by the definition (3.8) of Ω_0, in particular condition (3.5), it follows that

$$R_0(\omega_0) \geq R_0(\omega_0 + \varepsilon \nabla r(\omega_0)) = R_0(\omega_0) + \varepsilon \, \nabla r(\omega_0) \cdot \nabla R_0(\omega_0) + O(\varepsilon^2), \tag{8.2}$$

and hence $\nabla r(\omega_0) \cdot \nabla R_0(\omega_0) \leq 0$, which proves (3.9).

The proof of (3.10) and (3.11) involves the definition of a regular and twice continuously differential curve $\omega_r : (0, 1) \to \operatorname{int} \Omega$ with a unit tangent vector $\omega_r'(s) := d\omega_r(s)/ds$, $||\omega_r'(s)|| = 1$, such that

$$\omega_r(s_0) = \omega_0 \quad \text{for given } s_0 \in (0, 1), \tag{8.3}$$

$$r(\omega_r(s)) = r(\omega_0) \quad \text{for all } s \in (0, 1). \tag{8.4}$$

Note that the image of the curve ω_r lies on top of the level contour of r passing through ω_0. The existence of such curve is guaranteed by the twice continuously differentiability of r and the assumption that $\nabla r(\omega_0)$ is not zero.

Differentiation of (8.4) with respect to s and evaluated at s_0 gives

$$\nabla r(\omega_0) \cdot \omega_r'(s_0) = 0, \tag{8.5}$$

$$\omega_r'(s_0) \cdot \mathcal{H}(r(\omega_0)) \, \omega_r'(s_0) + \nabla r(\omega_0) \cdot \omega_r''(s_0) = 0, \tag{8.6}$$

where $\mathcal{H} := d^2/d\omega^2$ is the Hessian operator.

From the definition (3.8) of Ω_0, in particular condition (3.5), it follows that ω_0 maximizes R_0 on the boundary of the set $\{\upsilon \in \Omega : r(\upsilon) \geq r(\omega_0)\}$. The boundary is the $r(\omega_0)$-level contour of the function r and, by construction, coincides with the image of the curve ω_r, at least in a neighborhood of ω_0. Thus, s_0 locally maximizes $R_0(\omega_r(s))$ on the interval $(0, 1)$, and so

$$\nabla R_0(\omega_0) \cdot \omega_r'(s_0) = 0, \tag{8.7}$$

$$\omega_r'(s_0) \cdot \mathcal{H}(R_0(\omega_0)) \, \omega_r'(s_0) + \nabla R_0(\omega_0) \cdot \omega_r''(s_0) \leq 0. \tag{8.8}$$

From (8.5) and (8.7) it can be seen that both $\nabla r(\omega_0)$ and $\nabla R_0(\omega_0)$ are orthogonal to $\omega_r'(s_0)$. Since all three are vectors in the plane, it follows that $\nabla r(\omega_0)$ and $\nabla R_0(\omega_0)$ are parallel to one another, i.e., they are linear dependent. Hence, $\det(\nabla r(\omega_0), \nabla R_0(\omega_0)) = 0$, which proves (3.10).

To prove (3.11), note from (3.9) and (3.10) that $\nabla r(\omega_0)$ and $\nabla R_0(\omega_0)$ are not just parallel to one another but also point in exactly opposite directions, and so

$$\frac{\nabla r(\omega_0)}{||\nabla r(\omega_0)||} + \frac{\nabla R_0(\omega_0)}{||\nabla R_0(\omega_0)||} = 0. \tag{8.9}$$

This can be used to eliminate $\nabla R_0(\omega_0)$ from (8.8), which gives

$$\omega_r'(s_0) \cdot \mathcal{H}(R_0(\omega_0))\, \omega_r'(s_0) - \frac{||\nabla R_0(\omega_0)||}{||\nabla r(\omega_0)||} \nabla r(\omega_0) \cdot \omega_r''(s_0) \le 0. \tag{8.10}$$

Using (8.6) to subsequently eliminate $\nabla r(\omega_0) \cdot \omega_r''(s_0)$ from (8.10), we get

$$\omega_r'(s_0) \cdot \mathcal{H}(R_0(\omega_0))\, \omega_r'(s_0) + \frac{||\nabla R_0(\omega_0)||}{||\nabla r(\omega_0)||}\, \omega_r'(s_0) \cdot \mathcal{H}(r(\omega_0))\, \omega_r'(s_0) \le 0. \tag{8.11}$$

Without loss of generality we can orient the curve ω_r such that

$$\omega_r'(s_0) = ||\nabla r(\omega_0)||^{-1} \begin{pmatrix} -\partial r/\partial t \\ \partial r/\partial m \end{pmatrix}, \tag{8.12}$$

which by (8.9) is equivalent to

$$\omega_r'(s_0) = ||\nabla R_0(\omega_0)||^{-1} \begin{pmatrix} \partial R_0/\partial t \\ -\partial R_0/\partial m \end{pmatrix}. \tag{8.13}$$

Using (8.12) to substitute the first three occurrences of $\omega_r'(s_0)$ in (8.11), and using (8.13) to substitute the last $\omega_r'(s_0)$, we get

$$\begin{pmatrix} -\partial r/\partial t \\ \partial r/\partial m \end{pmatrix} \cdot \left(\mathcal{H}(R_0(\omega_0)) \begin{pmatrix} -\partial r/\partial t \\ \partial r/\partial m \end{pmatrix} + \mathcal{H}(r(\omega_0)) \begin{pmatrix} \partial R_0/\partial t \\ -\partial R_0/\partial m \end{pmatrix} \right) \le 0. \tag{8.14}$$

By just writing out in terms of vector and matrix components, one finds that

$$\mathcal{H}(R_0(\omega_0)) \begin{pmatrix} -\partial r/\partial t \\ \partial r/\partial m \end{pmatrix} + \mathcal{H}(r(\omega_0)) \begin{pmatrix} \partial R_0/\partial t \\ -\partial R_0/\partial m \end{pmatrix} = \nabla \det(\nabla r(\omega_0), \nabla R_0(\omega_0)). \tag{8.15}$$

Hence (8.14) is equivalent to (3.11).

8.2 On the geometric interpretation of Proposition 3.5

Here we show that condition (3.11) compares the curvatures of the level contours of the functions r and R_0 at ω_0. To this end, recall that for any regular and twice continuously differentiable curve $x\colon (0, 1) \to \mathbb{R}^2$ with a unit tangent vector $x'(s) := dx(s)/ds$, $||x'(s)|| = 1$, the curvature is defined as $k(s) := \det(x'(s), x''(s))$ (e.g., Guggenheimer 1977). The curvature of ω_r as defined in the proof of Proposition 3.5 is thus $k_r(s) := \det(\omega_r'(s), \omega_r''(s))$, which given the orientation in (8.12), is

$$k_r(s_0) = -||\nabla r(\omega_0)||^{-1}\, \nabla r(\omega_0) \cdot \omega_r''(s_0). \tag{8.16}$$

Using (8.6) to eliminate $\nabla r(\omega_0) \cdot \omega_r''(s_0)$ from this expression, we get

$$k_r(s_0) = ||\nabla r(\omega_0)||^{-1}\, \omega_r'(s_0) \cdot \mathcal{H}(r(\omega_0))\, \omega_r'(s_0). \tag{8.17}$$

Next we define the regular and twice continuously differential curve $\omega_{R_0} \colon (0, 1) \to \operatorname{int} \Omega$ with a unit tangent vector $\omega_{R_0}'(s) := d\omega_{R_0}(s)/ds$, $||\omega_{R_0}'(s)|| = 1$, and such that

$$\omega_{R_0}(s_0) = \omega_0 \quad \text{for } s_0 \in (0, 1), \tag{8.18}$$

$$R_0(\omega_{R_0}(s)) = R_0(\omega_0) \quad \text{for all } s \in (0, 1). \tag{8.19}$$

The image of ω_{R_0} coincides with the level contour of R_0 passing through ω_0, at least locally. The existence of the curve is again guaranteed by the twice continuously differentiability of R_0 and the assumption that $\nabla R_0(\omega_0)$ is not zero. Differentiation of (8.19) twice with respect to s and evaluated at s_0 gives

$$\omega_{R_0}'(s_0) \cdot \mathcal{H}(R_0(\omega_0))\, \omega_{R_0}'(s_0) + \nabla R_0(\omega_0) \cdot \omega_{R_0}''(s_0) = 0. \tag{8.20}$$

We orient ω_{R_0} in the same way as ω_r, so that in particular $\omega_{R_0}'(s_0) = \omega_r'(s_0)$. By (8.13), the curvature $k_{R_0}(s) := \det(\omega_{R_0}'(s), \omega_{R_0}''(s))$ evaluated at s_0 thus becomes

$$k_{R_0}(s_0) = ||\nabla R_0(\omega_0)||^{-1}\, \nabla R_0(\omega_0) \cdot \omega_{R_0}''(s_0). \tag{8.21}$$

Using (8.20) to eliminate $\nabla R_0(\omega_0) \cdot \omega_{R_0}''(s_0)$ from this expression, we get

$$k_{R_0}(s_0) = -||\nabla R_0(\omega_0)||^{-1}\, \omega_{R_0}'(s_0) \cdot \mathcal{H}(R_0(\omega_0))\, \omega_{R_0}'(s_0). \tag{8.22}$$

Using (8.17) and (8.22) to rewrite condition (8.11) in the proof of Proposition 3.5 in terms of curvatures, we get

$$k_r(s_0) \leq k_{R_0}(s_0). \tag{8.23}$$

In the proof of Proposition 3.5, expression (8.11)–(8.15), it can be seen that (3.11) is equivalent to (8.11), which now we have shown to be equivalent to (8.23), which that at s_0 the curvature of ω_r is less than the curvature of ω_{R_0}. Since the images of ω_r and ω_{R_0} locally coincide with the level contours of, respectively, r and R_0, we can rephrase this in terms of the curvatures of the level contours as was done in Sect. 3.

8.3 Proof of Proposition 4.1

In terms of λ, μ and ν, the conditions (3.9) and (3.10) can be written as

$$\gamma + m^2\,(m+\gamma)\,\lambda(t)\Big(\lambda(t)+\mu(m)-\nu(t)\Big) - t\,m\,(m+\gamma)\,\mu'(m) \le 0, \tag{8.24}$$

$$(m+\gamma)\Big(\mu(m)-\nu(t)\Big) + m\,\lambda(t)\Big(1+t\,(m+\gamma)\,\mu'(m)\Big) = 0, \tag{8.25}$$

from which we find (4.6) and (4.7).

8.4 Proof of Proposition 4.2

In terms of λ, μ and ν, the conditions (3.9) and (3.10) can be written as

$$-1 + m(m+\gamma)\,\lambda(t)\Big(\mu(m)-\nu(t)\Big) - t\,(m+\gamma)\,\mu'(m) \le 0, \tag{8.26}$$

$$(m+\gamma)\Big(\mu(m)-\nu(t)\Big) + m\,\lambda(t)\Big(1+t\,(m+\gamma)\,\mu'(m)\Big) = 0, \tag{8.27}$$

from which we find (4.8) and (4.9).

8.5 Proof of Proposition 4.3

First, let R_0 be given by (4.4). Then, the tangent vector (3.13) written out in terms of λ and μ and ν becomes

$$\left(\frac{A\,r\,R_0}{m(m+\gamma)}, \frac{-B\,r\,R_0}{m^2(m+\gamma)^2}\right)^{\top}, \tag{8.28}$$

with

$$A = m\,\lambda'(t)\Big(1+t\,(m+\gamma)\,\mu'(m)\Big) + (m+\gamma)\Big(m\,\lambda(t)\,\mu'(m)-\nu'(m)\Big), \tag{8.29}$$

$$B = (m+\gamma)^2\Big(m\,\mu'(m)-\mu(m)+\nu(t)\Big) + m^2\lambda(t)\Big(t\,(m+\gamma)\,\mu''(m)-1\Big). \tag{8.30}$$

Given $\lambda'(t) > 0$, $\mu'(t) > 0$, $\nu' < 0$, $\mu''(m) \ge 0$ and $\nu - \mu > \lambda$, we get the following estimates for A and B:

$$A > m\,\lambda'(t) > 0, \tag{8.31}$$

$$B > \gamma\,(2m+\gamma)\,\lambda(t) > 0. \tag{8.32}$$

Next, let R_0 be given by (4.5). Then, the tangent vector (3.13) written out in terms of λ and μ and ν becomes

$$\left(\frac{A\,r\,R_0}{m(m+\gamma)}, \frac{-B\,r\,R_0}{m(m+\gamma)^2}\right)^\top, \tag{8.33}$$

with

$$A = m\,\lambda'(t)\Big(1 + t\,(m+\gamma)\,\mu'(m)\Big) + (m+\gamma)\Big(m\,\lambda(t)\,\mu'(m) - \nu'(m)\Big), \tag{8.34}$$

$$\begin{aligned} B =& (m+\gamma)\Big((m+\gamma)\,\mu'(m) - \mu(m) + \nu(t)\Big) \\ &+ \lambda(t)\Big(-m+\gamma+t\,(m+\gamma)\Big(\gamma\,\mu'(m) + m\,(m+\gamma)\,\mu''(m)\Big)\Big). \end{aligned} \tag{8.35}$$

Given $\lambda'(t) > 0$, $\mu'(t) > 0$, $\nu' < 0$, $\mu''(m) \geq 0$ and $\nu - \mu > \lambda$, we get the following estimates for A and B:

$$A > m\,\lambda'(t) > 0, \tag{8.36}$$

$$B > 2\gamma\,\lambda(t) > 0. \tag{8.37}$$

Thus, for R_0 be given by (4.4) or (4.5), A and B are both strictly positive and so the vector components in (8.28) have opposite signs, and hence the tangent to Ω_0 has a negative slope.

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