Invasion implies substitution in ecological communities with class-structured populations

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Abstract

Long-term evolution of quantitative traits is classically and usefully described as the directional change in phenotype due to the recurrent fixation of new mutations. A formal justification for such continual evolution ultimately relies on the "invasion implies substitution" principle. Here, whenever a mutant allele causing a small phenotypic change can successfully invade a population, the ancestral (or wild-type) allele will be replaced, whereby fostering gradual phenotypic change if the process is repeated. It has been argued that this principle holds in a broad range of situations, including spatially and demographically structured populations experiencing frequency and density dependent selection under demographic and environmental fluctuations. However, prior studies have not been able to account for all aspects of population structure, leaving unsettled the conditions under which the "invasion implies substitution"-principle really holds. In this paper, we start by laying out a program to explore and clarify the generality of the "invasion implies substitution"-principle. Particular focus is given on finding an explicit and functionally constant representation of the selection gradient on a quantitative trait. Using geometric singular perturbation methods, we then show that the "invasion implies substitution"-principle generalizes to well-mixed and scalar-valued polymorphic multispecies ecological communities that are structured into finitely many demographic (or physiological) classes. The selection gradient is shown to be constant over the evolutionary timescale and that it depends only on the resident phenotype, individual growth-rates, population steady states and reproductive values, all of which are calculated from the resident dynamics. Our work contributes to the theoretical foundations of evolutionary ecology.

1 Introduction

A central theme in evolutionary biology is to understand how organisms have evolved to become adapted to their environment. Of particular relevance is to understand adaptation to biotic environments which contain, and are altered by, the interactions of the organism with members of its own and other species (Pásztor et al., 2016; Estrela et al., 2018). Examples of such interactions permeate the biological world, they include competition for resources, mate choice, helping behavior and cultural learning to name a few, and will here be collectively referred to as social interactions. Social interactions, however, may lead to complex frequency and/or density-dependent evolutionary dynamics. It may thus be felt that in general not much can be said about the evolutionary adaptive trajectory of social traits.

Notwithstanding this complexity, it has been extensively argued that when mutations cause only small changes to the phenotype under selection, the evolutionary trajectory of a phenotype can be continual under directional selection, proceeding by a gradual, small-step by small-step transformation of the phenotype under focus (e.g., Hamilton, 1964; Eshel, 1983; Metz et al., 1995; Geritz et al., 1998; Rousset and Billiard, 2000; Leturque and Rousset, 2002; Rousset, 2004; Rousset and Ronce, 2004; Geritz, 2005; Rousset, 2006; Dercole and Rinaldi, 2008; Durinx et al., 2008; Lehmann and Rousset, 2014; Dercole and Geritz, 2016). Such a paradigmatic Darwinian process (e.g., Dawkins, 1997) relies on the "invasion implies substitution"-principle, which is the ultimate fixation in the population of any mutant that is being favored by selection when initially rare. The "invasion implies substitution"-principle has been suggested to hold not only for arbitrary social interactions, but also in cases where populations are spatially and demographically (physiologically) structured and subject to demographic and environmental fluctuations (Rousset, 2004; Geritz, 2005; Durinx et al., 2008; Lehmann and Rousset, 2014) and has been called a "gift from God" (Hamilton, 1988).

The intuitive argument for justifying "invasion implies substitution"-principle relies on considering two alleles, a wild-type (resident) allele coding for some phenotype and a mutant allele coding for some closely similar phenotype. The argument is then that the dynamics of an appropriately weighted average mutant allele frequency p in the population is much slower than the dynamics of all other variables governing the demographic and genetic make-up of the population, such us population densities and genetic associations like relatedness or linkage disequilibria (see Figure 1 panels A and B and Rousset, 2004, p. 196 and p. 206-207 for an early general discussion of this argument). Consequently, the genetic and ecological variables (collectively referred to as population dynamical variables) that operate in fast population dynamical time can be assumed constant at the slow evolutionary time at which the mutant frequency p changes, rendering selection essentially frequency-independent. More precisely, the expected change Δp in (weighted) mutant frequency p is supposed to follow a dynamical equation like

$$\Delta p = \delta \mathrm{V}(p) S + O(\delta^2), \tag{1}$$

where δ is the phenotypic deviation between mutant and resident phenotype, and $\mathrm{V}(p)$ is frequency-dependent but always a positive measure of genetic variation at the loci under selection, e.g., for a well-

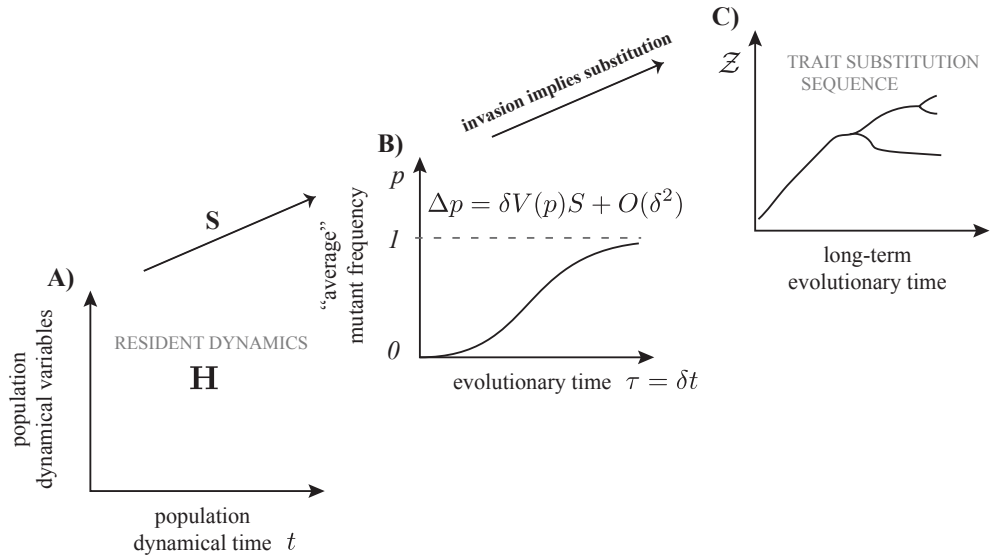

Figure 1: The three timescales that are relevant for the "invasion implies substitution"-principle. A) The population dynamical timescale at which all fast genetic and demographic (ecological) dynamical variables converge to their steady state. Here, the individual growth-rate matrix **H** determines the resident dynamics. B) The evolutionary timescale at which the (weighted average) mutant frequency p changes, and where the mutant allele may or may not substitute its ancestral resident allele. Here, the fast population dynamical variables are at their steady state and thus constant. C) The long-term evolutionary timescale at which the phenotype under selection changes (also called meso-evolutionary timescale, Metz, 2011). The trait under selection takes values in the trait space $\mathcal{Z}$. This panel gives the timescale of the trait substitution sequence where each individual trait substitution is defined as an invasion implies substitution event.

mixed population this is simply $p(1-p)$ with p being the average mutant frequency in the population. Moreover, S is a frequency-independent selection gradient, which is a function of the fast population dynamical variables and is calculated for a resident population. Whenever the selection gradient S is non-zero, (1) says that if mutant frequency p increases when rare it substitutes the resident; that is, it substitutes its ancestral phenotype. This is the "invasion implies substitution"-principle.

Decoupling the slow evolutionary variable p from the fast population dynamical variables, however, is not straightforward in complex communities that exhibit population structure. When individuals are structured into different demographic classes such as age or size classes, or when individuals inhabit different spatial locations, it is not obvious how to define the mutant frequency and on which timescale does it operate (Leturque and Rousset, 2002; Rousset and Ronce, 2004; Rousset, 2006). Indeed, class-specific mutant frequencies and thus also the mean mutant frequency in the population are usually not purely slow evolutionary variables (Leturque and Rousset, 2002; Rousset and Ronce, 2004). Moreover, when individuals are structured into continuous or countably infinite age-classes and habitats (Metz and Diekmann, 1986; Diekmann et al., 1998, 2001; Rousset, 2006), population dynamical variables such as population densities or genetic associations are not necessarily fast either (Greiner et al., 1994; Rousset, 2006; Gyllenberg, 2007). In both situations a standard timescale separation method is not readily applicable, or, may not even be possible.

Despite of these complications, it has been conjectured that the "invasion implies substitution"-principle

nevertheless holds in structured populations (Rousset, 2004; Durinx et al., 2008; Metz and de Kovel, 2013), more specifically, in populations with finite number of demographic and spatial classes where individuals are characterized by scalar-valued traits (Rousset, 2004). The central step here follows from the realization that when the mutant frequency in the population p is defined as the class-specific reproductive weighted average frequency (e.g., Stubblefield and Seger, 1990; Taylor, 1990; Leturque and Rousset, 2002; Rousset, 2004; Lehmann and Rousset, 2014; Grafen, 2015), it is a purely slow evolutionary variable operating in purely slow evolutionary time. Consequently, this suggests that the dynamics of the weighted average frequency p can be generically cast in the form (1) and moreover with a selection gradient that can be partitioned according to the following generic form

$$S = \mathbf{v}\left[\frac{\partial \mathbf{H}}{\partial z_{\text{self}}} + \sum_{\omega\in\mathcal{G}}\sum_{\mathscr{c}\in\mathcal{D}} \frac{\partial \mathbf{H}}{\partial z_{\text{others in } \omega,\mathscr{c}}}\mathbf{R}_{\text{others in } \omega,\mathscr{c}}\right]\mathbf{n}. \tag{2}$$

Here, the matrix $\mathbf{H}$ is a resident growth-rate matrix whose elements $h_{\mathscr{a}\mathscr{b}}$ give the rates at which individuals are produced into demographic class $\mathscr{a} \in \mathcal{D}$ by a single resident individual in demographic class $\mathscr{b} \in \mathcal{D}$ and $\mathcal{D}$ denotes the demographic class-space. This matrix has $\mathbf{v}$ and $\mathbf{n}$ as leading left and right eigenvectors giving, respectively, the resident individual reproductive values and steady states (see Figure 2 for the partition of S). Because eigenvectors can be scaled arbitrarily, in an alternative but equivalent formulation the class-specific population densities $\mathbf{n}$ can be replaced by a probability distribution of a demographic class, i.e., by class frequencies. The partial derivatives $\frac{\partial \mathbf{H}}{\partial z_{\text{self}}}$ and $\frac{\partial \mathbf{H}}{\partial z_{\text{others in } \omega,\mathscr{c}}}$ are taken with respect to the phenotype (more precisely, with respect to the contribution of an allele on the phenotype) of the individual whose growth-rate we are considering, and with respect to the phenotype of individuals in all the spatial and demographic classes over which we are summing $\omega \in \mathcal{G}, \mathscr{c} \in \mathcal{D}$, respectively, where $\mathcal{G}$ denotes the spatial class space (i.e., the number of distinct spatial locations an individual can inhabit). These derivatives are usually interpreted as fitness effects caused by mutations (see also Figure 2), and the matrix $\mathbf{R}_{\text{others in } \omega,\mathscr{c}}$ weights these effects by the average genealogical relationship between individuals that occupy the same spatial and demographic class as the individual whose growth-rate is being considered, and individuals in spatial class $\omega \in \mathcal{G}$ and demographic class $\mathscr{c} \in \mathcal{D}$. That is, the elements of $\mathbf{R}_{\text{others in } \omega,\mathscr{c}}$ are neutral relatedness coefficients (Rousset, 2004). To our knowledge, no generalizations of (2) to more generally structured populations are known.

Equation (2) is consistent with all previous work on the "invasion implies substitution"-principle. In particular, two categories of demographically unstructured population models have treated the "invasion implies substitution"-principle in depth. The first category are well-mixed (panmictic) population models with fluctuating demography caused by density and frequency-dependent selection (Geritz, 2005; Meszéna et al., 2005; Dercole and Rinaldi, 2008; Dercole and Geritz, 2016), where population density is the single population dynamical variable. These models include scalar-valued (Dercole and Rinaldi, 2008; Dercole and Geritz, 2016) and vector-valued traits (Geritz, 2005; Meszéna et al., 2005), arbitrary (Dercole and Rinaldi, 2008) or tightly clustered polymorphisms (Meszéna et al., 2005), as well as populations that are part of a larger ecological community (Dercole and Rinaldi, 2008). The "invasion implies substitution"-principle was here proven by singularly perturbing (Fenichel, 1979; Wiggins, 1994; Jones, 1995; Hek,

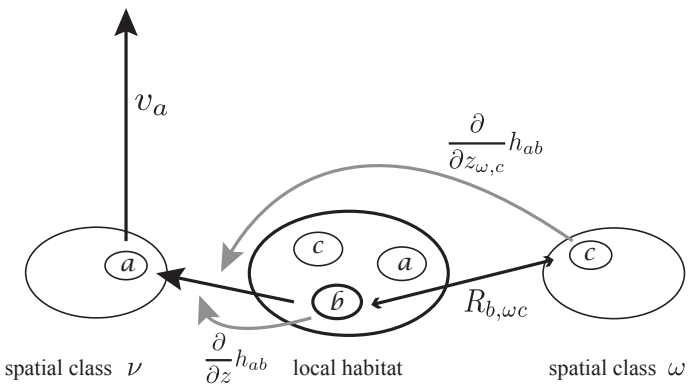

Figure 2: The partitioning of the selection gradient S as an inclusive fitness effect. Suppose that, as a thought experiment, the deviation between the mutant and resident phenotype δ is set to zero for all mutant individuals in the population (i.e., all individuals have the same phenotype). Then, suppose a "button" is pressed so that all mutant individuals in the population "switch" to expressing the small δ deviation. Pressing the button can (marginally) affect the production rate h_{ab} of class a offspring of a randomly sampled mutant individual residing in demographic class b in a given discrete spatial location (denoted as "local habitat" in the figure) in two ways. First, it can affect the production "directly" because the individual in class b expresses the δ deviation, which results in marginal effect $\frac{\partial}{\partial z_{\text{self}}} h_{ab}$ on self. Second, the mutant can also be affected "indirectly" due to social (frequency or density dependent) interactions with other mutant individuals expressing the δ deviation, which results in marginal effect $\frac{\partial h_{ab}}{\partial z_{\text{others in } \omega,c}}$ multiplied by the (relative) probability that individuals in ω, c also have the mutation (which is conditional on the individual in class b), i.e., the probability $R_{b,\text{others in } \omega,c}$ where $\mathbf{R}_{\text{others in } \omega c} = (R_{b,\omega c})_{a \in \mathcal{D}}$. Because there are n_b individuals in class b and the reproductive value of the produced individuals in a is v_a, the selection gradient in (2) is obtained from $v_a[\frac{\partial}{\partial z} h_{ab} + \frac{\partial}{\partial z_{\omega,c}} h_{ab} R_{b,\omega c}] n_b$ by summing over all possible spatial and demographic classes.

2010; Kuehn, 2015) the slow evolutionary dynamics in order to obtain an approximation for the mutant frequency dynamics resulting from small but nonzero deviations between mutant and resident phenotypes (Dercole and Rinaldi, 2008; Dercole and Geritz, 2016, see an alternative proof of Geritz, 2005). Such perturbation analysis is essential in situations where fast population dynamical variables (e.g. population density) may not persist under the perturbation caused by the invasion of a mutant phenotype (Geritz et al., 2002) and may lead e.g. to a catastrophic extinction of the population (Ferriere, 2000; Gyllenberg and Parvinen, 2001; Parvinen, 2016). The selection gradient was then shown to take the form $S = \frac{\partial h}{\partial z_{\text{self}}}$ (Dercole and Rinaldi, 2008; Dercole and Geritz, 2016), where population density comes into play as an argument of the growth-rate function.

The second category of demographically unstructured models (Wakeley, 2003; Roze and Rousset, 2003; Wakeley and Takahashi, 2004; Rousset, 2004, 2006) assumes that the population exhibits spatial or group structure with limited dispersal, but as the population is not assumed to experience demographic fluctuations all spatial locations are identical and so all individual belong to the same demographic class. Thus, the single population dynamical variable is the genealogical relationship between individuals within a group (that is of constant and finite size), i.e., the relatedness between group members. Invasion implies substitution was shown to hold by using the diffusion approximation method for two timescales developed in Ethier and Nagylaki (1980, 1988), where one scales up a finite population model by letting the number of groups to go to infinity while the phenotypic deviation between mutant and resident phenotypes goes to zero. Because the only population dynamical variable is density-independent relatedness (whose

dynamics is further linear), relatedness itself depends smoothly on the evolving phenotype, and so the aforementioned results are robust against small but nonzero phenotypic deviations caused by the invasion of a mutant phenotype (for instance, no bifurcation leading to population extinction can occur). This method was applied in the island model of dispersal (i.e., the spatial structure considered in Wright, 1931) for the discrete-time Wright-Fisher model (Wakeley, 2003) and for the Moran model (Wakeley and Takahashi, 2004), whereas (Roze and Rousset, 2003; Rousset, 2004, 2006) showed that the "invasion implies substitution"-principle holds for a much larger class of discrete-time population models including diploid populations (in the absence of over and under-dominance), and showed that the selection gradient can be expressed as $S = \frac{\partial h}{\partial z_{\text{self}}} + \frac{\partial h}{\partial z_{\text{others}}} R_{\text{others}}$ (Roze and Rousset, 2003; Rousset, 2004, 2006). A related model considers isolation by distance (Rousset, 2006). Here the timescale separation is obtained by utilizing the observation that the genealogical relationships between individuals in different spatial locations can be captured by studying the proportions of distributions of coalescence times (Slatkin, 1991). The selection gradient was then shown to take the form $S = \frac{\partial h}{\partial z_{\text{self}}} + \sum_{\omega \in \mathcal{G}} \frac{\partial h}{\partial z_{\text{others in } \omega}} R_{\text{others in } \omega}$ and since the population is structured into countably infinite number of spatial locations, the population dynamical variable (relatedness coefficient) is of a countably infinite dimension.

Some studies have also discussed invasion implies substitution in demographically structured populations in both well-mixed and group-structured populations with limited dispersal. First and most recently, Lion (2018a,b) discusses the "invasion implies substitution"-principle for a haploid well-mixed population that is assumed demographically class-structured and part of a larger ecological community. Here, the focus is given to the dynamics of the trait mean for a polymorphic trait that is tightly clustered around its mean. Consequently, the timescale separation arguments were made in terms of aggregate variables such as trait means and variances instead of the full distribution of mutant frequencies, which should actually be considered in a full proof of the "invasion implies substitution"-principle, but nevertheless it was shown that the selection gradient takes form $S = \mathbf{v} \frac{\partial \mathbf{H}}{\partial z_{\text{self}}} \mathbf{n}$. Second, the "invasion implies substitution"-principle has been considered in the island model of dispersal with finite but demographically fluctuating local population sizes (Rousset, 2004; Rousset and Ronce, 2004; Lehmann et al., 2016); division into demographic classes such as age or size classes (Rousset, 2004); and sex-classes with different ploidy levels (Roze and Rousset, 2004) and sex-specific imprinting (Van Cleve et al., 2010). Here, it is argued that the timescale separation between the mutant frequency and the local genetic and demographic structure holds when the mutant frequency is defined as the average frequency weighted by (demographically) class-specific reproductive values (Taylor, 1990; Leturque and Rousset, 2002; Rousset, 2004) and using the timescale separation arguments of Ethier and Nagylaki (1980, 1988), in which case the selection gradient can be expressed under the form $S = \mathbf{v} \left[\frac{\partial \mathbf{H}}{\partial z_{\text{self}}} + \frac{\partial \mathbf{H}}{\partial z_{\text{others}}} \mathbf{R}_{\text{other}} \right] \mathbf{n}$ (Rousset, 2004; Lehmann et al., 2016). Similarly to the spatially structured model without demographic fluctuations, these models contain only one spatial location and so relatedness only needs to be calculated within groups that belong to the same demographic class (notice no summation in the selection gradient). However, no explicit, step-by-step full proof of the "invasion implies substitution"-principle has actually been detailed for these class-structured models (beyond invoking that Ethier and Nagylaki, 1980, 1988 applies to them, e.g., Rousset, 2004, p. 196) and thus remains wanting in the literature. In particular, because each group

consists of individuals that fluctuate between different demographic classes the growth-rate functions as well as relatedness can be density-dependent under certain scenarios, which requires a more detailed analysis on the robustness of the evolutionary mutant frequency dynamics under small but non-zero perturbations caused by the invasion of the mutant.

In summary, while the "invasion implies substitution"-principle seems to be well established for several biological scenarios, there is no completely detailed proof specifying all steps for the case of demographically and spatially class-structured populations. More generally, it remains to explore and clarify the following sets of questions pertaining to the adaptive dynamics of closely similar phenotypes, and which could be called the "invasion implies substitution"-principle *program*.

(I) What is the validity and generality of the "invasion implies substitution"-principle in structured populations with respect to the trait space, the demographic class space, and the spatial class space (respectively $\mathcal{Z}, \mathcal{D}, \mathcal{G}$)?

(II) If the principle holds in a given model, (a) what conditions must the resident growth-rate matrix (or operator) $\mathbf{H}$ satisfy, and (b) can the evolutionary dynamics of the mutant phenotype systematically be expressed as in (1)?

(III) If the mutant dynamics satisfy (1), can we find an explicit expression for the selection gradient S as in (2), that is, can we generically express S in terms of (a) individual reproductive values $\mathbf{v}$, (b) steady states $\mathbf{n}$, and (c) relatedness $\mathbf{R}$, all of which can be determined from resident quantities such as the growth-rate matrix $\mathbf{H}$ evaluated at the attractor of the ecological community?

Our aim in this paper is to contribute to this program (or quest). Because answering the above question is complex and has ramification with many evolutionary models, not everything can be answered in a single paper. We thus consider here a scalar-valued quantitative trait under selection in a clonally reproducing (or haploid) well-mixed population structured into finitely many demographic classes residing in a larger ecological community (allowing for arbitrary eco-evolutionary feedback), and prove positive answers to all three questions (I)-(III) posed above. In so doing, we lay out in detail the concept of singular perturbation theory and multiple timescale analysis (Fenichel, 1979; Wiggins, 1994; Jones, 1995; Hek, 2010; Kuehn, 2015), which we apply to limited dispersal in a subsequent paper. Because we formulate our model in continuous-time and from the outset assume that the population size is large, our treatment also complements previous well-mixed demographically class-structured models (in particular those implied by the models in Rousset, 2004), which are started with discrete-time and finite total population size formulation and use scaling of both time and system size to obtain the desired timescale separation (Ethier and Nagylaki, 1980, 1988; Rousset, 2004).

The rest of this paper is organized as follows. We start Section 2 by constructing a continuous-time population model that completely describes the population as well as the evolutionary dynamics of the ecological community. We then move on to study the mutant-resident dynamics in situations where the mutant and its ancestral resident phenotype are closely similar (Section 3). In Section 4 we proceed to prove the "invasion implies substitution"-principle by decoupling the slow evolutionary dynamics given

by the average mutant frequency weighted by class reproductive values from the fast dynamics given by the population dynamical variables. We conclude by discussing related work and the overall relevance of our results to evolutionary ecology (Section 5).

2 Model

Consider an infinitely large haploid population where each individual is characterized by a single one-dimensional (scalar-valued) continuous trait. The phenotypic value of the trait of each individual is assumed fixed during its life and individuals are structured into finitely many demographic classes (Taylor, 1990; Charleworth, 1994), e.g. age or size classes, which in contrast to the phenotype may change throughout their life. The population of interest may also be part of a greater ecological community - individuals of the population interact with individuals from other species (e.g. predator-prey community), which may also be structured into different phenotypes and demographic classes.

Preliminaries Let $\mathcal{Z} \subset \mathbb{R}$ denote the space of phenotypes, $\mathcal{D}$ the set of $m \in \mathbb{N}_+$ distinct demographic classes where m is finite, and take time to be continuous. As the present model has no spatial structure, and thus no spatial classes, we omit the term "demography" in front of the word class. Note that $\mathcal{Z}$ and $\mathcal{D}$ jointly give the full description of the life-history of individuals in the population (birth, maturation and death) and hence jointly define a so-called individual-level state space (Metz and Diekmann, 1986; Diekmann, 2002).

Moreover, suppose that the population, at least initially, is polymorphic with respect to the trait under focus with all in all k distinct alleles segregating (each coding for a distinct phenotype), all of which define the resident population. However, because we will assume that one (and only one) of the k alleles undergoes a mutation giving rise to a new phenotype denoted $z_{\mathrm{M}} \in \mathcal{Z}$ (M stands for mutant), we single out its ancestral phenotype and call it the ancestral resident phenotype $z_{\mathrm{R}} \in \mathcal{Z}$, or simply, the resident. After mutation, the population thus consists of a mutant allele (with phenotype z_{M}), a resident allele (with phenotype $z_{\mathrm{R}} \in \mathcal{Z}$), as well as $k-1$ other alleles, each with their respective phenotypes. Since, under our assumptions, there is a one to one relationship between allele and phenotype, we will generally just speak of mutant and resident phenotypes.

It will be useful to distinguish individuals not only by their phenotype but also the class they are in. For example, a mutant that is in class $a \in \mathcal{D}$ will be identified with $z_{\mathrm{M},a}$. We emphasise that $z_{\mathrm{R},a}$ and $z_{\mathrm{M},a}$ take phenotypic value $z_{\mathrm{R}}, z_{\mathrm{M}} \in \mathcal{Z}$, respectively, for all $a \in \mathcal{D}$, and that this notation is introduced (only) for a bookkeeping purpose, that is, to keep track of individuals moving in time through the individual-level state space. Finally, to make a distinction between (resident individuals in) resident dynamics and (resident individuals in) mutant-resident dynamics, we will drop out the subscript denoting residents (R) whenever we are discussing ecological communities where the mutant phenotypes are absent.

We now first present a model for a polymorphic resident ecological community where the mutant phenotype is assumed absent (Section 2.1). Then, we extend the model to a situation where one of the

phenotypes has undergone a mutation resulting in an arbitrary mutant phenotype and express the dynamical system in terms of class-specific mutant frequencies (Section 2.2). Finally, in Section 2.3, we give several consistency relations and properties that relate mutant-resident dynamics to resident dynamics, which will play a central role in deriving the main results of this paper.

2.1 Resident dynamics

Let $\mathbf{n} = (n_a)_{a\in\mathcal{D}} \in \mathbb{R}_+^m$ denote the vector of densities (number of individuals per unit space) of (ancestral) resident individuals in all the possible classes the individuals can be in, with element $n_a \in \mathbb{R}_+$ denoting the density of resident individuals in class $a \in \mathcal{D}$. Similarly, $\mathbf{z} = (z_a)_{a\in\mathcal{D}} \in \mathcal{Z}^m$ denotes the resident phenotype vector where element z_a identifies individuals in class $a \in \mathcal{D}$ with a phenotype $z \in \mathcal{Z}$. The density vector $\mathbf{n}_\mathrm{P} \in \mathbb{R}_+^l$ collects, for each class, the density of the other $k-1$ resident phenotypes in the population of the focal species and the densities of the rest of the ecological community. Hence, if we have a community with a single species $l = (k-1)m$, otherwise $l > (k-1)m$.

The resident dynamics is given by the set of ordinary differential equations

$$\begin{aligned} \dot{\mathbf{n}} &= \mathbf{H}(z, \mathbf{z}, \mathbf{n}, \mathbf{n}_\mathrm{P})\mathbf{n} \\ \dot{\mathbf{n}}_\mathrm{P} &= \mathbf{P}(\mathbf{z}, \mathbf{n}, \mathbf{n}_\mathrm{P}), \end{aligned} \tag{3}$$

where the dot " $\cdot$ " above the density vectors $\mathbf{n}$ and $\mathbf{n}_\mathrm{P}$ denotes the time derivative "$\frac{\mathrm{d}}{\mathrm{d}t}$". The matrix $\mathbf{H} = \left(h_{ab}\right)_{a,b\in\mathcal{D}} \in \mathbb{R}^{m\times m}$ is the (ancestral) resident growth-rate matrix where entry $h_{ab}(z, \mathbf{z}, \mathbf{n}, \mathbf{n}_\mathrm{P})$ is a sufficiently smooth growth-rate function giving the rate at which a single individual of class b produces individuals of class a. We emphasise that the first argument $z \in \mathcal{Z}$ in the growth-rate matrix $\mathbf{H}(z, \mathbf{z}, \mathbf{n}, \mathbf{n}_\mathrm{P})$ identifies the phenotype of the individual whose growth-rate we are considering, while all the remaining arguments describe the environment that the individual finds itself in. The matrix $\mathbf{P} \in \mathbb{R}^{l\times l}$ is the growth-rate matrix of the rest of the resident population and the ecological community and is also a function of the environment that the individuals find themselves in. For notational convenience, especially when it is clear from the context, we will drop from the growth-rate matrices and functions all arguments that describe the environment, for example, we may write $\mathbf{H}(z)$ instead of $\mathbf{H}(z, \mathbf{z}, \mathbf{n}, \mathbf{n}_\mathrm{P})$ and $\mathbf{P}$ instead of $\mathbf{P}(\mathbf{z}, \mathbf{n}, \mathbf{n}_\mathrm{P})$.

We note that all the growth-rate functions presented in this paper are constructed by assuming an infinitely large well-mixed ecological community, where individuals are assumed to undergo demographic individual-level processes on a Poissonian basis; the demographic processes can be either asocial where individuals react by themselves e.g., dying or moving from one age class to another, or social, resulting from random encounters of pairs of individuals. The probability of any higher order encounter vanishes in continuous-time models. However, all growth-rate functions can be non-linear and of any complexity as we allow for arbitrary frequency and/or density dependent (pairwise) interactions. Different underlying assumptions on the encounters between individuals is possible, facilitating e.g. multiplayer games (Weibull, 1995), but are not dealt with in this paper.

Steady state of the resident dynamics Throughout the paper we assume that there exists an equilibrium point $(\hat{\mathbf{n}}, \hat{\mathbf{n}}_{\mathrm{P}}) \in \mathbb{R}_+^{m+l}$ to which the community given by (3) converges to and then stays at. Importantly, this equilibrium is assumed to be hyperbolically stable, i.e. the real part of the dominant eigenvalue of the linearized system (3) evaluated at the equilibrium is negative and bounded away from zero (Hirsch et al., 1974). However, we allow the system (3) to contain multiple non-negative equilibria or other attractors at which the community could potentially reside. Assuming multiple equilibria or other attractors is not problematic when considering evolutionary dynamics because the so-called *tube theorem* (Geritz et al., 2002) excludes "attractor switching" for mutant-resident dynamics with closely similar phenotypes. That is, the dynamics of the mutant with a similar phenotype to a resident will never evolve to an alternative attractor. In Section 5 we discuss how our results can be extended to more complicated attractors than equilibria.

2.2 Mutant-resident dynamics

We now introduce the mutant phenotype $z_{\mathrm{M}} \in \mathcal{Z}$ into the resident population. Let $\mathbf{n}_{\mathrm{R}} = (n_{\mathrm{R},a})_{a\in\mathcal{D}} \in \mathbb{R}_+^m$ and $\mathbf{n}_{\mathrm{M}} = (n_{\mathrm{M},a})_{a\in\mathcal{D}} \in \mathbb{R}_+^m$ denote the vectors of densities and $\mathbf{z}_{\mathrm{R}} = (z_{\mathrm{R},a})_{a\in\mathcal{D}} \in \mathcal{Z}^m$ and $\mathbf{z}_{\mathrm{M}} = (z_{\mathrm{M},a})_{a\in\mathcal{D}} \in \mathcal{Z}^m$ the vectors of phenotypes of (ancestral) residents and mutants, respectively, in all the possible classes the individuals can be in. The mutant-resident dynamics is then given by

$$\begin{aligned}
\dot{\mathbf{n}}_{\mathrm{M}} &= \mathbf{G}(z_{\mathrm{M}}, \mathbf{z}_{\mathrm{R}}, \mathbf{z}_{\mathrm{M}}, \mathbf{n}_{\mathrm{R}}, \mathbf{n}_{\mathrm{M}}, \mathbf{n}_{\mathrm{P}})\mathbf{n}_{\mathrm{M}} \\
\dot{\mathbf{n}}_{\mathrm{R}} &= \mathbf{G}(z_{\mathrm{R}}, \mathbf{z}_{\mathrm{R}}, \mathbf{z}_{\mathrm{M}}, \mathbf{n}_{\mathrm{R}}, \mathbf{n}_{\mathrm{M}}, \mathbf{n}_{\mathrm{P}})\mathbf{n}_{\mathrm{R}} \\
\dot{\mathbf{n}}_{\mathrm{P}} &= \mathbf{R}(\mathbf{z}_{\mathrm{R}}, \mathbf{z}_{\mathrm{M}}, \mathbf{n}_{\mathrm{R}}, \mathbf{n}_{\mathrm{M}}, \mathbf{n}_{\mathrm{P}}),
\end{aligned} \tag{4}$$

where $\mathbf{G} = \left(g_{ab}\right)_{a,b\in\mathcal{D}} \in \mathbb{R}^{m\times m}$ is the growth-rate matrix of individuals in the mutant-resident population, such that $\mathbf{G}(x) := \mathbf{G}(x, \mathbf{z}_{\mathrm{R}}, \mathbf{z}_{\mathrm{M}}, \mathbf{n}_{\mathrm{R}}, \mathbf{n}_{\mathrm{M}}, \mathbf{n}_{\mathrm{P}})$ is the growth-rate matrix of a phenotype $x \in \{z_{\mathrm{M}}, z_{\mathrm{R}}\}$ and that each entry $g_{ab}(x)$ is a sufficiently smooth growth-rate function giving the rate at which a single individual with phenotype $x \in \{z_{\mathrm{M}}, z_{\mathrm{R}}\}$ in class $b \in \mathcal{D}$ produces individuals in class $a \in \mathcal{D}$. It is clear from this formulation that as we have assumed the growth-rate matrix $\mathbf{G}$ and its arguments be identical for mutants and residents (except the first), we have assumed that mutants and residents experience the exact same environment and thus the only difference in their growth-rate is due to their own phenotype. In particular, every individual is surrounded by equal number (density) of mutants and residents. Similarly to the second line of of the resident dynamics (3), $\mathbf{R} \in \mathbb{R}^{l\times l}$ is the growth-rate matrix of the $k-1$ remaining resident phenotypes in each class and of the rest of the ecological community.

Relative mutant-resident dynamics Because we are interested in the relative dynamics of mutants $z_{\mathrm{M}} \in \mathcal{Z}$ and (ancestral) residents $z_{\mathrm{R}} \in \mathcal{Z}$, it will be convenient to change the dynamical variables by considering the frequency of mutants $p_{\mathrm{M},a} = \frac{n_{\mathrm{M},a}}{n_a}$ in class $a \in \mathcal{D}$, where $n_a = n_{\mathrm{M},a} + n_{\mathrm{R},a}$ is the total density of mutants and residents in class $a \in \mathcal{D}$. The vectors $\mathbf{p} = (p_{\mathrm{M},a})_{a\in\mathcal{D}} \in [0,1]^m$ and $\mathbf{n} = (n_a)_{a\in\mathcal{D}} \in \mathbb{R}_+^m$ are thus the vectors for class-specific mutant frequencies and class-specific total densities of (mutant and ancestral resident) individuals, respectively. We emphasise that since we are interested in the relative

dynamics of mutants and their ancestral residents, the mutant frequency $p_{\mathrm{M},a}$ is defined with respect to mutants and their ancestral residents in class $a \in \mathcal{D}$, not all k resident phenotypes present in the population.

We can now rewrite the mutant-resident dynamics (4) in terms of the class-specific mutant frequencies $\mathbf{p}$ and the class-specific total population densities $\mathbf{n}$ as

$$\begin{aligned}
\dot{\mathbf{p}} &= \mathbf{F}(z_{\mathrm{M}}, \mathbf{z}_{\mathrm{R}}, \mathbf{z}_{\mathrm{M}}, \mathbf{p}, \mathbf{n}, \mathbf{n}_{\mathrm{P}})\mathbf{p} \\
\dot{\mathbf{n}} &= \bar{\mathbf{G}}(\mathbf{z}_{\mathrm{R}}, \mathbf{z}_{\mathrm{M}}, \mathbf{p}, \mathbf{n}, \mathbf{n}_{\mathrm{P}})\mathbf{n} \\
\dot{\mathbf{n}}_{\mathrm{P}} &= \mathbf{R}(\mathbf{z}_{\mathrm{R}}, \mathbf{z}_{\mathrm{M}}, \mathbf{n}_{\mathrm{R}}, \mathbf{n}_{\mathrm{M}}, \mathbf{n}_{\mathrm{P}}),
\end{aligned} \tag{5}$$

where $\bar{\mathbf{G}} = (\bar{g}_{ab})_{a,b\in\mathcal{D}}$, with $\bar{g}_{ab} = g_{ab}(z_{\mathrm{M}})p_{\mathrm{M},b} + g_{ab}(z_{\mathrm{R}})p_{\mathrm{R},b}$, is the average mutant-resident growth-rate matrix, and where $\mathbf{F} = (f_{ab})_{a,b\in\mathcal{D}} \in \mathbb{R}^{m\times m}$ is the relative growth-rate matrix (see Appendix 6.1 for a relative growth rate matrix for an arbitrary phenotype). The entries of the relative growth-rate matrix for mutants $\mathbf{F}(z_{\mathrm{M}}) := \mathbf{F}(z_{\mathrm{M}}, \mathbf{z}_{\mathrm{R}}, \mathbf{z}_{\mathrm{M}}, \mathbf{p}, \mathbf{n}, \mathbf{n}_{\mathrm{P}})$ are obtained by differentiation

$$\begin{aligned}
\dot{p}_{\mathrm{M},a} &= \frac{\mathrm{d}}{\mathrm{d}t}\left(\frac{n_{\mathrm{M},a}}{n_a}\right) = \frac{\dot{n}_{\mathrm{M},a}n_a - n_{\mathrm{M},a}\dot{n}_a}{n_a^2} \\
&= \frac{1}{n_a}\left[\dot{n}_{\mathrm{M},a} - p_{\mathrm{M},a}\dot{n}_a\right] \\
&= \sum_b \frac{n_b}{n_a} g_{ab}(z_{\mathrm{M}})p_{\mathrm{M},b} - p_{\mathrm{M},a}\sum_b \frac{n_b}{n_a}\bar{g}_{ab}, \qquad \forall a \in \mathcal{D},
\end{aligned} \tag{6}$$

where we have used equations (4) and (5) and the definition of class mutant frequencies $p_{\mathrm{M},a}$. Motivated by Lion (2018b, Appendix A.3), it will be useful to rewrite (6) by subtracting and adding a term $\sum_b \frac{n_b}{n_a}\bar{g}_{ab}p_{\mathrm{M},b}$, to obtain

$$\dot{p}_{\mathrm{M},a} = \sum_b \frac{n_b}{n_a}\left[g_{ab}(z_{\mathrm{M}}) - \bar{g}_{ab}\right]p_{\mathrm{M},b} + \sum_b \frac{n_b}{n_a}\bar{g}_{ab}p_{\mathrm{M},b} - p_{\mathrm{M},a}\sum_b \frac{n_b}{n_a}\bar{g}_{ab} \qquad \forall a \in \mathcal{D}. \tag{7}$$

This allows us to partition the mutant relative growth-rate matrix as

$$\mathbf{F}(z_{\mathrm{M}}) = \mathbf{F}^{\mathrm{sel}}(z_{\mathrm{M}}) + \bar{\mathbf{F}}^{\mathrm{pc}}, \tag{8a}$$

where $\mathbf{F}^{\mathrm{sel}} = (f_{ab}^{\mathrm{sel}})_{a,b\in\mathcal{D}} \in \mathbb{R}^{m\times m}$ and $\bar{\mathbf{F}}^{\mathrm{pc}} = (\bar{f}_{ab}^{\mathrm{pc}})_{a,b\in\mathcal{D}} \in \mathbb{R}^{m\times m}$ with entries, respectively, given by

$$f_{ab}^{\mathrm{sel}}(z_{\mathrm{M}}) = \frac{n_b}{n_a}\left[g_{ab}(z_{\mathrm{M}}) - \bar{g}_{ab}\right] \tag{8b}$$

and

$$\bar{f}_{ab}^{\mathrm{pc}} = \begin{cases} \frac{n_b}{n_a}\bar{g}_{ab} & \forall b \neq a \\ -\sum_{c\neq a}\frac{n_c}{n_a}\bar{g}_{ac}, & \text{for } b = a. \end{cases} \tag{8c}$$

Notice that $f_{ab}^{\mathrm{sel}}(z_{\mathrm{M}})$ is proportional to the difference between mutant $g_{ab}(z_{\mathrm{M}})$ and average growth-rates $\bar{g}_{ab}$

and thus captures the effect of selection (hence the superscript "sel") on mutant allele frequency change. The second term $\bar{f}^{\mathrm{pc}}_{a\mathscr{b}}$ is proportional only to average growth-rates $\bar{g}_{a\mathscr{b}}$ and hence captures non-selective effects on allele frequency change due to transitions between classes. Since the relative growth-rate of an individual due to the term $\bar{f}^{\mathrm{pc}}_{a\mathscr{b}}$ is non-selective and thus independent of ones phenotype (see also Appendix 6.1), the argument present e.g., in $f^{\mathrm{sel}}_{a\mathscr{b}}(z_{\mathrm{M}})$ is not included in $\bar{f}^{\mathrm{pc}}_{a\mathscr{b}}$, but it should nevertheless be kept in mind that $\bar{\mathbf{F}}^{\mathrm{pc}}$ depends both on mutant and resident traits. Such non-selective transitions between classes nevertheless affect the dynamics of the mutant frequency, for instance if one class of individuals, say newborns (or individuals living in a good habitat) have higher reproductive success than older individuals (individuals living in bad habitat). Such deterministic change of allele frequency due to non-selective forces have generally been referred to as changes due to "transmission" (following Barton and Turelli, 1991; Kirkpatrick et al., 2002), since they result from alleles changing contexts (e.g., from good habitat to bad habitat, from young to old individual; see Kirkpatrick et al., 2002 for more details on the concept of the context of an allele and a discussion of transmission as an evolutionary force). When the different contexts an allele can reside in are demographic classes, the changes in allele frequency due to transmission have been called "passive changes" (Grafen, 2015; Lion, 2018a,b) and we adhere to this terminology (hence the superscript "pc").

2.3 Properties of growth-rates

In this section we present three properties that relate mutant-resident dynamics (4) to resident dynamics (3) and then we apply them to the mutant relative growth-rate matrix (8). These properties and their applications play a central role in Section 3 when discussing mutant-resident dynamics for closely similar phenotypes and in Section 4 when proving our main result. The consistency relation given below is fully analogous to the relation given in (Geritz et al., 2002; Dercole, 2016; Dercole and Geritz, 2016) and the proposition given below is an analogue to a property derived for unstructured populations in (Meszéna et al., 2005; Dercole, 2016).

Consistency relations:

$$\begin{aligned}\mathbf{G}(x,\mathbf{z}_{\mathrm{R}},\mathbf{z}_{\mathrm{M}},\mathbf{n}_{\mathrm{R}},\mathbf{n}_{\mathrm{M}},\mathbf{n}_{\mathrm{P}})\Big|_{\substack{z_{\mathrm{R}}=z\\ z_{\mathrm{M}}=z}} &= \mathbf{H}(x,\mathbf{z},\mathbf{n},\mathbf{n}_{\mathrm{P}})\\ \mathbf{R}(\mathbf{z}_{\mathrm{R}},\mathbf{z}_{\mathrm{M}},\mathbf{n}_{\mathrm{R}},\mathbf{n}_{\mathrm{M}},\mathbf{n}_{\mathrm{P}})\Big|_{\substack{z_{\mathrm{R}}=z\\ z_{\mathrm{M}}=z}} &= \mathbf{P}(\mathbf{z},\mathbf{n},\mathbf{n}_{\mathrm{P}}),\end{aligned} \tag{9}$$

for any $x \in \mathscr{Z}$. This relation says that the growth-rate of any individual from any population and species in the ecological community, when all (other) individuals in the population are of the same phenotype $z \in \mathscr{Z}$, is its growth-rate in a resident ecological community (3) where $\mathbf{n} = \mathbf{n}_{\mathrm{R}} + \mathbf{n}_{\mathrm{M}}$.

Corollary:

$$\begin{aligned}\frac{\partial}{\partial z_{\mathrm{M}}}\mathbf{G}(z_{\mathrm{M}},\mathbf{z}_{\mathrm{R}},\mathbf{z}_{\mathrm{M}},\mathbf{n}_{\mathrm{R}},\mathbf{n}_{\mathrm{M}},\mathbf{n}_{\mathrm{P}})\Big|_{\substack{z_{\mathrm{R}}=z\\ z_{\mathrm{M}}=z}} &= \frac{\partial}{\partial z}\mathbf{H}(z,\mathbf{z},\mathbf{n},\mathbf{n}_{\mathrm{P}})\\ \frac{\partial}{\partial z_{\mathrm{M}}}\mathbf{G}(z_{\mathrm{R}},\mathbf{z}_{\mathrm{R}},\mathbf{z}_{\mathrm{M}},\mathbf{n}_{\mathrm{R}},\mathbf{n}_{\mathrm{M}},\mathbf{n}_{\mathrm{P}})\Big|_{\substack{z_{\mathrm{R}}=z\\ z_{\mathrm{M}}=z}} &= \mathbf{0},\end{aligned} \tag{10}$$

This property follows immediately from the Consistency relation describing the effect that a mutant phenotype of an individual has on its own growth-rate. Trivially, residents don't have a mutant phenotype and so there is no such effect for the resident growth matrix. The same is true also for the matrix $\mathbf{R}$, but as we don't need the Corollary for $\mathbf{R}$ we haven't included it here.

Proposition:

$$\frac{\partial}{\partial z_{\mathrm{M},a}}\mathbf{G}(x,\mathbf{z}_{\mathrm{R}},\mathbf{z}_{\mathrm{M}},\mathbf{n}_{\mathrm{R}},\mathbf{n}_{\mathrm{M}},\mathbf{n}_{\mathrm{P}})\Big|_{\substack{z_{\mathrm{R}}=z\\ z_{\mathrm{M}}=z}} = \frac{\partial}{\partial z_a}\mathbf{H}(x,\mathbf{z},\mathbf{n},\mathbf{n}_{\mathrm{P}})p_{\mathrm{M},a}, \tag{11}$$

for any $x \in \mathcal{Z}$ and for all $a \in \mathcal{D}$. This property says that the effect that all mutants in class $a \in \mathcal{D}$ in the mutant-resident community (4) have on the individual growth-rate (left-hand side of (11)), is equal to the effect that all individuals in class $a \in \mathcal{D}$ in the resident community (3) have on the individual growth-rate, weighted with the probability that given a random pairwise encounter with an individual of class $a \in \mathcal{D}$, it is a mutant (right-hand side of (11)). This property is a consequence of the growth-rate function being constructed in terms of pairwise interactions between individuals (generalized mass action law), and is a direct generalization of the property 4 given for unstructured populations in (Dercole, 2016) (see also Meszéna et al., 2005).

Properties of relative growth-rates Here we apply the above properties (9)-(11) to the mutant relative growth rate matrix (8). Substituting the consistency relation (9) into (8) implies that the selection component of the relative growth-rate matrix $\mathbf{F}^{\mathrm{sel}} = \mathbf{0}$ is a null matrix for phenotypic equality between mutant and its (ancestral) resident, therefore

$$\mathbf{F}(z_{\mathrm{M}})\Big|_{\substack{z_{\mathrm{R}}=z\\ z_{\mathrm{M}}=z}} = \bar{\mathbf{F}}^{\mathrm{pc}}\Big|_{\substack{z_{\mathrm{R}}=z\\ z_{\mathrm{M}}=z}}, \tag{12a}$$

where

$$f_{ab}(z_{\mathrm{M}})\Big|_{\substack{z_{\mathrm{R}}=z\\ z_{\mathrm{M}}=z}} = \bar{f}^{\mathrm{pc}}_{ab}\Big|_{\substack{z_{\mathrm{R}}=z\\ z_{\mathrm{M}}=z}} = \begin{cases}\frac{n_b}{n_a}h_{ab}(z) & \forall b \neq a\\ -\sum_{c\neq a}\frac{n_c}{n_a}h_{ac}(z), & \text{for } b = a.\end{cases}, \tag{12b}$$

for all $a, b \in \mathcal{D}$. We thus confirm that under phenotypic equality, selection (i.e., the component $\mathbf{F}^{\mathrm{sel}}(z_{\mathrm{M}})$) plays no role (as it should not) and that the change in class-specific mutant frequencies is non-trivial and purely determined by the matrix $\bar{\mathbf{F}}^{\mathrm{pc}}$. That is, under phenotypic equality it is the "passive changes" that determines the dynamics of class-specific mutant frequencies (Taylor, 1990; Stubblefield and Seger, 1990; Charleworth, 1994; Grafen, 2015; Lion, 2018a,b).

The Corollary (10) and the Proposition (11) immediately imply, respectively, that

$$\frac{\partial}{\partial z_{\mathrm{M}}} f^{\mathrm{sel}}_{ab}(z_{\mathrm{M}})\Big|_{\substack{z_{\mathrm{R}}=z\\ z_{\mathrm{M}}=z}} = \frac{n_b}{n_a}\frac{\partial}{\partial z} h_{ab}(z)(1-p_{\mathrm{M},b}) \tag{13a}$$

$$\frac{\partial}{\partial z_{\mathrm{M},c}} f^{\mathrm{sel}}_{ab}(z_{\mathrm{M}})\Big|_{\substack{z_{\mathrm{R}}=z\\ z_{\mathrm{M}}=z}} = 0, \tag{13b}$$

for all $a, b, c \in \mathcal{D}$. Analogously to above, both properties describe the effect that a mutant phenotype has on the mutant relative growth-rate. The property (13a) follows from the fact that the effect of a mutant phenotype on ones own growth-rate is $\frac{\partial}{\partial z} h_{ab}(z)$ if one is a mutant and $\frac{\partial}{\partial z} h_{ab}(z) p_{\mathrm{M},b}$ if one is an average (random) individual in class $b \in \mathcal{D}$. The property (13b) in turn follows from the fact that in a well-mixed population all individuals experience the exact same social environment and hence the effect that mutants in class $c \in \mathcal{D}$ have on a mutant growth-rate and an average growth-rate are equal.

3 Mutant-resident dynamics for nearby phenotypes

In this section, we will study the relative mutant-resident dynamics (5) for closely similar phenotypes. To prove the "invasion implies substitution"-principle by using a timescale separation argument, we wish that for closely similar phenotypes the mutant frequency in the population is a much slower dynamical variable than all other dynamical variables in the model. If so, the fast dynamical variables would then have enough time to reach their steady state (or at least to be sufficiently close to it) and thus could be considered as constant arguments of the (much slower) evolutionary dynamics of the mutant frequency. To check the timescale of all dynamical variables present in the relative mutant-resident dynamics (5), let $z_{\mathrm{M}} = z_{\mathrm{R}} + \delta$ and let us Taylor expand (5) up to the second order about $\delta = 0$,

$$\begin{aligned}
\dot{\mathbf{p}} &= \mathbf{F}(z_{\mathrm{M}})\Big|_{\delta=0}\mathbf{p} + \delta\frac{\mathrm{d}}{\mathrm{d}\delta}\mathbf{F}\Big|_{\delta=0}\mathbf{p} + O(\delta^2)\\
\dot{\mathbf{n}} &= \bar{\mathbf{G}}\Big|_{\delta=0}\mathbf{n} + \delta\frac{\mathrm{d}}{\mathrm{d}\delta}\bar{\mathbf{G}}\Big|_{\delta=0}\mathbf{n} + O(\delta^2)\\
\dot{\mathbf{n}}_{\mathrm{P}} &= \mathbf{R}\Big|_{\delta=0} + \delta\frac{\mathrm{d}}{\mathrm{d}\delta}\mathbf{R}\Big|_{\delta=0} + O(\delta^2),
\end{aligned} \tag{14}$$

which can be rewritten using (9) and (12) as

$$\begin{aligned}
\dot{\mathbf{p}} &= \bar{\mathbf{F}}^{\mathrm{pc}}_0\mathbf{p} + \delta\frac{\mathrm{d}}{\mathrm{d}\delta}\mathbf{F}\Big|_{\delta=0}\mathbf{p} + O(\delta^2)\\
\dot{\mathbf{n}} &= \mathbf{H}(z)\mathbf{n} + \delta\frac{\mathrm{d}}{\mathrm{d}\delta}\bar{\mathbf{G}}\Big|_{\delta=0}\mathbf{n} + O(\delta^2)\\
\dot{\mathbf{n}}_{\mathrm{P}} &= \mathbf{P} + \delta\frac{\mathrm{d}}{\mathrm{d}\delta}\mathbf{R}\Big|_{\delta=0} + O(\delta^2)
\end{aligned} \tag{15}$$

where $\bar{\mathbf{F}}^{\mathrm{pc}}_0 := \bar{\mathbf{F}}^{\mathrm{pc}}|_{\delta=0}$ is as given in (12). From these equations, we can see that as all variables $\mathbf{p}, \mathbf{n}$ and $\mathbf{n}_{\mathrm{P}}$ fluctuate at a rate dominated by the terms of order $O(1)$; that is, they are all fast population dynamical variables. Or, in other words, none of the dynamical variables $\mathbf{p}, \mathbf{n}$ nor $\mathbf{n}_{\mathrm{P}}$ are (at least not purely) slow evolutionary variables dominated by the terms of order $O(\delta)$. This is true in particular for the class-specific mutant frequencies $\mathbf{p}$ and also for the mean mutant frequency $p_{\mathrm{M}} = \sum_a \frac{n_a}{n} p_{\mathrm{M},a}$ in the

population (Appendix 6.2). Since there are no purely slow evolutionary variables, a timescale separation can't be readily performed.

In the next Section 3.1, we show that an average mutant frequency weighted by class reproductive values is the (purely) slow evolutionary variable enabling a timescale separation argument to be made. In the following Section 3.2, we then find the steady state to which the fast population dynamical variables approach to, and then in Section 4 we use these results to prove the "invasion implies substitution"-principle.

3.1 Class reproductive value weighted average mutant frequency

To find a purely slow evolutionary variable that tracks changes in class mutant frequencies $\mathbf{p}$, thus tracking also the mean mutant frequency in the population p_{M}, we take an average of $\mathbf{p}$ over all $p_{\mathrm{M},a}$ with weights chosen such that the change of this weighted average mutant frequency vanishes under phenotypic equality. For the moment, let $\boldsymbol{\alpha}$ be an arbitrary vector of weights normalized such as $\sum_{a\in\mathcal{D}} \alpha_a = 1$, and lets denote the average mutant frequency weighted by $\boldsymbol{\alpha}$ with

$$p_\alpha := \boldsymbol{\alpha}\mathbf{p} = \sum_{a\in\mathcal{D}} \alpha_a p_{\mathrm{M},a}. \tag{16}$$

Because we are interested in the dynamics of p_α, we follow the steps taken in Lion (2018b, Appendix A.3), and differentiate with respect to time t and obtain

$$\begin{aligned} \dot{p}_\alpha &= \dot{\boldsymbol{\alpha}}\mathbf{p} + \boldsymbol{\alpha}\dot{\mathbf{p}} \\ &= \left[\dot{\boldsymbol{\alpha}} + \boldsymbol{\alpha}\bar{\mathbf{F}}^{\mathrm{pc}}\right]\mathbf{p} + \boldsymbol{\alpha}\mathbf{F}^{\mathrm{sel}}(z_{\mathrm{M}})\mathbf{p}, \end{aligned} \tag{17}$$

where we have used (5) and (8). Now, the class reproductive values are defined such that for any frequency distribution $\mathbf{p}$ they "cancel" the class transitions due to "passive changes" or transmission between classes (Taylor, 1990; Leturque and Rousset, 2002; Grafen, 2015; Lehmann and Rousset, 2014; Lion, 2018b), rendering the dynamics of the weighted frequency (17) solely due to terms of class transitions due to selection. This requirement is satisfied precisely when the term in the brackets in (17) is zero for all $\mathbf{p}$, which is true whenever

$$\dot{\boldsymbol{\alpha}} = -\boldsymbol{\alpha}\bar{\mathbf{F}}^{\mathrm{pc}}, \tag{18}$$

where $\bar{\mathbf{F}}^{\mathrm{pc}}$ is as in (8). Note that as $\bar{f}^{\mathrm{pc}}_{aa} = -\sum_{b\neq a} \bar{f}^{\mathrm{pc}}_{ab}$, the matrix $\bar{\mathbf{F}}^{\mathrm{pc}}$ is the infinitesimal generator matrix for a (backward) continuous-time mutant-resident Markov chain $\boldsymbol{\alpha}$ on the state space $\mathcal{D}$. Using (18) as the definition for class reproductive values, the dynamics of the weighted mutant frequency (17) reduces to

$$\dot{p}_\alpha = \boldsymbol{\alpha}\mathbf{F}^{\mathrm{sel}}(z_{\mathrm{M}})\mathbf{p}. \tag{19}$$

We have thus obtained that since $\boldsymbol{\alpha}$ by definition satisfies (18), the dynamics of the weighted mutant frequency p_α is determined purely by the selection component of the relative growth rate matrix as given in (19) (see for an alternative derivation in terms of individual reproductive values, Appendix 6.5.4). Interestingly, as we have made no assumptions on the magnitude of δ, the above equation is valid for arbitrary phenotypic values $z_{\mathrm{M}}, z_{\mathrm{R}} \in \mathcal{Z}$ and thus for arbitrary strength of selection. Moreover, because $\mathbf{F}^{\mathrm{sel}}|_{\delta=0} = \mathbf{0}$ is a null matrix (12), the dynamics of p_α under phenotypic similarity (δ small) is

$$\dot{p}_\alpha = \delta \boldsymbol{\alpha} \frac{\mathrm{d}}{\mathrm{d}\delta} \mathbf{F}^{\mathrm{sel}}(z_{\mathrm{M}})\Big|_{\delta=0} \mathbf{p} + O(\delta^2). \tag{20}$$

Because the dynamics of p_α for closely similar phenotypes is dominated by the terms $O(\delta)$, we will be able to track mutant frequencies $\mathbf{p}$ (and p_{M}) purely in slow evolutionary time by studying the δ-term of p_α. The average mutant frequency weighted by class reproductive values p_α is thus a well suited proxy for the slow evolutionary dynamics of p_{M}.

Class reproductive values as fast and slow variables Whenever the class reproductive values $\boldsymbol{\alpha}$ are defined as in (18), the phenotypic values z_{M} and z_{R} as well as the fluctuations in the dynamical variables $\mathbf{p}, \mathbf{n}, \mathbf{n}_{\mathrm{P}}$, may be arbitrary. The class reproductive values are therefore defined both in fast and slow time (depending whether the dynamical variables are at their steady state or not) as well as for any strength of selection (which is determined by the magnitude of δ). If the variables $\mathbf{n}, \mathbf{n}_{\mathrm{P}}$ under phenotypic equality $\delta = 0$ are at their steady state $\hat{\mathbf{n}}, \hat{\mathbf{n}}_{\mathrm{P}}$ and thus constant in time, the steady state class reproductive values $\hat{\boldsymbol{\alpha}}$ are solvable from

$$\mathbf{0} = \hat{\boldsymbol{\alpha}} \hat{\mathbf{F}}_0^{\mathrm{pc}}, \tag{21}$$

where $\hat{\mathbf{F}}_0^{\mathrm{pc}} = \bar{\mathbf{F}}_0^{\mathrm{pc}}(\mathbf{z}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_{\mathrm{P}})$. The class reproductive values $\hat{\boldsymbol{\alpha}}$ can thus be defined as the left eigenvector of $\hat{\mathbf{F}}^{\mathrm{pc}}$ associated with the eigenvalue 0. This is the standard definition of the class reproductive values that have long been used as allele frequency weights in class-structured models (e.g., Stubblefield and Seger, 1990; Taylor, 1990; Taylor and Frank, 1996; Leturque and Rousset, 2002; Rousset and Ronce, 2004; Rousset, 2004). Therefore, $\hat{\alpha}_a$ can be interpreted as the asymptotic probability (looking backward in time) that the ancestral lineage of a random individual was in class $a \in \mathcal{D}$. That is, $\hat{\alpha}_a$ gives the long-term contribution of all genes in class $a \in \mathcal{D}$ to the future composition of the population (e.g., Rousset and Ronce, 2004, p. 131; Lehmann, 2014, eq. 7; Lion, 2018b, p. 624).

3.2 Steady states and the critical and perturbed manifolds

In Section 3.1, we found that the slow evolutionary dynamics of the weighted average mutant frequency p_α (19) is a function of the fast population dynamical variables $\boldsymbol{\alpha}, \mathbf{p}, \mathbf{n}$ and $\mathbf{n}_{\mathrm{P}}$, and that under phenotypic similarity (δ small) the dynamics of p_α (20) is dominated by the terms of order $O(\delta)$ and the dynamics of $\boldsymbol{\alpha}, \mathbf{p}, \mathbf{n}$ and $\mathbf{n}_{\mathrm{P}}$ by the terms of order $O(1)$. Under phenotypic equality ($\delta = 0$) it is thus sufficient to

study

$$
\begin{aligned}
\dot{\boldsymbol{\alpha}} &= -\boldsymbol{\alpha}\bar{\mathbf{F}}_0^{\mathrm{pc}}(\mathbf{z},\mathbf{n},\mathbf{n}_{\mathrm{P}}) \\
\dot{\mathbf{p}} &= \bar{\mathbf{F}}_0^{\mathrm{pc}}(\mathbf{z},\mathbf{n},\mathbf{n}_{\mathrm{P}})\mathbf{p} \\
\dot{\mathbf{n}} &= \mathbf{H}(z,\mathbf{z},\mathbf{n},\mathbf{n}_{\mathrm{P}})\mathbf{n} \\
\dot{\mathbf{n}}_{\mathrm{P}} &= \mathbf{P}(\mathbf{z},\mathbf{n},\mathbf{n}_{\mathrm{P}}),
\end{aligned}
\tag{22}
$$

where we used (15), (19) and where we have for clarity included all the arguments. Therefore, in fast population dynamical time, the variables $(\boldsymbol{\alpha},\mathbf{p},\mathbf{n},\mathbf{n}_{\mathrm{P}})$ fluctuate and are expected to reach their steady state while the weighted mutant frequency p_α stays constant. The steady state $(\hat{\boldsymbol{\alpha}},\hat{\mathbf{p}},\hat{\mathbf{n}},\hat{\mathbf{n}}_{\mathrm{P}})$ of (22) must, by definition, satisfy

$$
\begin{aligned}
\mathbf{0} &= \hat{\boldsymbol{\alpha}}\bar{\mathbf{F}}_0^{\mathrm{pc}}(\mathbf{z},\hat{\mathbf{n}},\hat{\mathbf{n}}_{\mathrm{P}}) \\
\mathbf{0} &= \bar{\mathbf{F}}_0^{\mathrm{pc}}(\mathbf{z},\hat{\mathbf{n}},\hat{\mathbf{n}}_{\mathrm{P}})\hat{\mathbf{p}} \\
\mathbf{0} &= \mathbf{H}(z,\hat{\mathbf{n}},\hat{\mathbf{n}}_{\mathrm{P}})\hat{\mathbf{n}} \\
\mathbf{0} &= \mathbf{P}(\hat{\mathbf{n}},\hat{\mathbf{n}}_{\mathrm{P}}).
\end{aligned}
\tag{23}
$$

We recall from Section 2.1 that the equilibrium solution $(\hat{\mathbf{n}},\hat{\mathbf{n}}_{\mathrm{P}})$ for the bottom two equations exists and is hyperbolically stable (by assumption), and from Section 3.1 we know that the steady state $\hat{\boldsymbol{\alpha}}$ exists and can be calculated from (21). The remaining task is to find the steady state $\hat{\mathbf{p}}$, which can be solved from

$$
\bar{\mathbf{F}}_0^{\mathrm{pc}}(\mathbf{z},\hat{\mathbf{n}},\hat{\mathbf{n}}_{\mathrm{P}})\hat{\mathbf{p}} = \mathbf{0} \tag{24}
$$

$$
\Longleftrightarrow
$$

$$
\sum_{\mathit{b}} \bar{f}_{\mathit{ab}}^{\mathrm{pc}}(\mathbf{z},\hat{\mathbf{n}},\hat{\mathbf{n}}_{\mathrm{P}})\Big|_{\delta=0}\hat{p}_{\mathrm{M},\mathit{b}} = \sum_{\mathit{b}} \frac{n_{\mathit{b}}}{n_{\mathit{a}}} h_{\mathit{ab}}(z,\mathbf{z},\hat{\mathbf{n}},\hat{\mathbf{n}}_{\mathrm{P}})(\hat{p}_{\mathrm{M},\mathit{b}} - \hat{p}_{\mathrm{M},\mathit{a}}) = 0 \qquad \forall \mathit{a} \in \mathcal{D}, \tag{25}
$$

and is given by

$$
\hat{\mathbf{p}} = (\hat{p}_{\mathrm{M},1},\ldots,\hat{p}_{\mathrm{M},m}) = (p,\ldots,p), \tag{26}
$$

where the class-specific mutant frequencies $p_{\mathrm{M},\mathit{a}}$ in all classes $\mathit{a} \in \mathcal{D}$ are equal. Notice that any value of p (biologically meaningful values lie between 0 and 1) gives a solution to (24) and hence the complete solution to (24) consists of infinite number of equilibria (which lie on a line; note that such a degenerate solution results from the fact that $\bar{\mathbf{F}}_0^{\mathrm{pc}}$ is a non-invertible matrix, Appendix 6.3). The exact value of $p \in [0,1]$ to which the class mutant frequencies $p_{\mathrm{M},\mathit{a}}$ approach to, $\forall \mathit{a} \in \mathcal{D}$, depends on the initial condition $\mathbf{p}(t=0)$. Interestingly, since by definition $p_\alpha(t) = \boldsymbol{\alpha}(t)\mathbf{p}(t)$ for all t as given in (16), and since under phenotypic equality the weighted average frequency is constant in fast population dynamical time ($\dot{p}_\alpha = 0$ as shown in Section 3.1, but note that in slow time p_α is no longer a constant), we must have that $\boldsymbol{\alpha}(0)\mathbf{p}(0) = p_\alpha(0) = p_\alpha(t) = \lim_{t\to\infty} p_\alpha(t) = \sum_{\mathit{a}} \hat{\alpha}_{\mathit{a}}\hat{p}_{\mathrm{M},\mathit{a}} = p$, and so $\hat{p}_{\mathrm{M},\mathit{a}} = p = p_\alpha(t)$ for all

$a \in \mathcal{D}$ and for all t; that is, the asymptotic mutant allele frequency in each class is equivalent to the reproductive value weighted mutant frequency.

We have thus obtained that whenever the mutant and resident phenotypes are equal $\delta = 0$, the dynamics given by system (22) approaches in fast population dynamical time a steady state $(\hat{\boldsymbol{\alpha}}, \hat{\mathbf{p}}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_{\mathrm{P}})$, which is solved from (23). We represent the infinite number of equilibrium points $(\hat{\boldsymbol{\alpha}}, \hat{\mathbf{p}}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_{\mathrm{P}})$ satisfying (23) as the set

$$\mathcal{M}_0 = \{(\hat{\boldsymbol{\alpha}}, \hat{\mathbf{p}}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_{\mathrm{P}}) \in \ \Delta^m \times [0,1]^m \times \mathbb{R}_+^{m+l} \mid \hat{p}_{\mathrm{M},a} = p_\alpha \ \forall a \in \mathcal{D}\}, \tag{27}$$

where Δ^m is the mth simplex and the subscript 0 indicates that we are studying the dynamics for the case where $\delta = 0$ (see Figure 3, top panel). The set $\mathcal{M}_0$ is the so-called critical (or equilibrium) manifold (Jones 1995, Definition 1, p. 49; Kuehn 2015, p. 12, see also Appendix 6.4.2 and recall that a manifold is here a sub-space of the original state space). This $\mathcal{M}_0$ manifold defines in fast population dynamical time the set of equilibrium (or critical) points to which the dynamical system with phenotypic equality $\delta = 0$ approaches to. As such, it can be thought of as the state space for the average weighted mutant frequency p_α when $\delta = 0$ (see Figure 3). Because $(\hat{\mathbf{n}}, \hat{\mathbf{n}}_{\mathrm{P}})$ is hyperbolic and the critical manifold $\mathcal{M}_0$ is compact (the set of points are bounded and closed) consisting of a neutral line of equilibria, it follows that $\mathcal{M}_0$ is compact and a normally hyperbolic invariant manifold (Appendix 6.4.2). Roughly speaking, invariant manifold is normally hyperbolic if the dynamics near the manifold is governed by the hyperbolicity condition while the dynamics on the manifold is neutral and thus invariant.

Slow manifold As elucidated above, the critical manifold $\mathcal{M}_0$ is compact and normally hyperbolic, and therefore the results of Fenichel (1971, 1974, 1977, 1979, see also Appendix 6.4 and the references within) guarantee that a perturbed manifold $\mathcal{M}_\delta$, the so-called slow manifold (Hek, 2010; Jones, 1995), for the mutant-resident dynamics under phenotypic closeness exists, is close to, and has identical stability properties as $\mathcal{M}_0$ (see also Figure 3, bottom panels). This slow manifold $\mathcal{M}_\delta$ is thus a set of points that are invariant under the flow of the full mutant-resident dynamics for small but nonzero δ (unlike in $\mathcal{M}_0$, however, the points in $\mathcal{M}_\delta$ are not equilibria), while in the neighborhood of $\mathcal{M}_\delta$ and $\mathcal{M}_0$ the dynamics of the system (22) are equivalent. In other words, because the dynamics under phenotypic equality given by (22) approaches the critical manifold $\mathcal{M}_0$, so does the dynamics under phenotypic closeness approach the slow manifold $\mathcal{M}_\delta$ (see Figure 3 and also, e.g., Jones 1995, Theorem 3, p. 62 and Theorem 6, p. 74). Moreover, the dynamics of p_α when restricted to $\mathcal{M}_0$ (in slow evolutionary time) and the dynamics of p_α when restricted to $\mathcal{M}_\delta$ or to its neighborhood (in fast and slow time) are also equivalent (see a more detailed discussion in Appendix 6.4). This result plays a fundamental role in Section 4, where we prove the "invasion implies substitution"-principle by studying the singularly perturbed slow evolutionary dynamics of p_α.

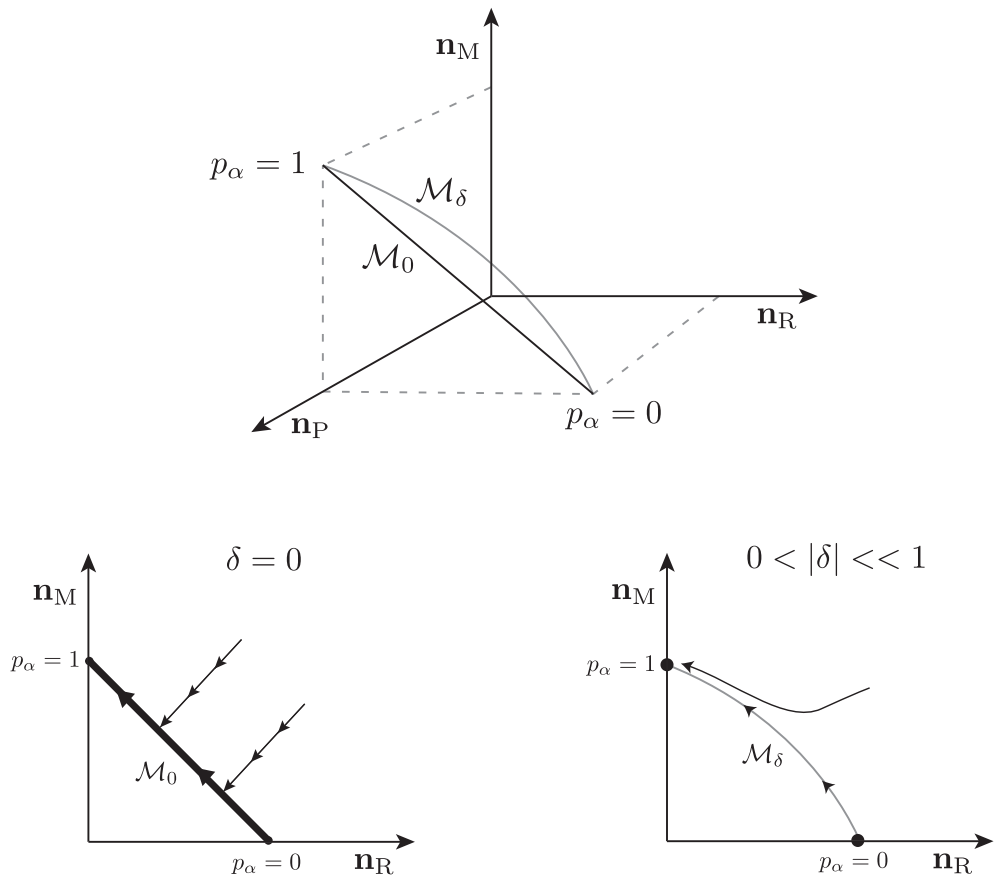

Figure 3: **Top panel:** Critical and slow manifolds $\mathcal{M}_0$ and $\mathcal{M}_\delta$, respectively. The critical manifold $\mathcal{M}_0$ is obtained from the mutant-resident dynamics under phenotypic equality ($\delta = 0$) by solving (23) and it consists of a line (infinite number) of equilibria. For the system (5) where δ is small but nonzero there exists a slow manifold $\mathcal{M}_\delta$, which is close to $\mathcal{M}_0$ and has the same dynamical properties as $\mathcal{M}_0$ (see bottom panels). **Bottom left panel:** The fast population (31) and slow evolutionary (32) dynamics of the singular system where $\delta = 0$. The thin lines with arrows represent the fast dynamical convergence given by (31) to $\mathcal{M}_0$ (where class-specific mutant frequencies are the weighted frequencies p_α), and the thick line with arrows represents the slow evolutionary dynamics of p_α given by (32) on $\mathcal{M}_0$ (in this example mutant frequency increases from 0 to 1). **Bottom right panel:** The mutant-resident dynamics (29) or (30) where δ is small but nonzero. The results of Fenichel (1979) say that since the (fast) dynamics for $\delta = 0$ (bottom left panel) approaches $\mathcal{M}_0$ so does the dynamics for small but non-zero δ approach $\mathcal{M}_\delta$. Moreover, the dynamics of p_α on $\mathcal{M}_\delta$ and its neighborhood, is equivalent of the (slow) dynamics of p_α on $\mathcal{M}_0$ (left panel).

4 Invasion implies substitution

We now prove the "invasion implies substitution"-principle for a model presented in this paper whose resident dynamics is given in (3). We prove the principle by separating the timescales at which the various dynamical variables of the mutant-resident model (4) operate by using the weighted average mutant frequency p_α. Because the dynamics of p_α is a function of class reproductive values $\boldsymbol{\alpha}$, mutant frequencies $\mathbf{p}$, (ancestral) resident densities $\mathbf{n}$ and the densities $\mathbf{n}_\mathrm{P}$ of the other resident phenotypes and the rest of the ecological community, the complete mutant-resident dynamics for arbitrary phenotypic values $z_\mathrm{R}, z_\mathrm{M} \in \mathcal{Z}$ (δ arbitrary) can be written by extending (5) as:

$$\begin{aligned}
\dot{p}_\alpha &= \boldsymbol{\alpha}\mathbf{F}^{\mathrm{sel}}(z_\mathrm{M}, \mathbf{z}_\mathrm{R}, \mathbf{z}_\mathrm{M}, \mathbf{p}, \mathbf{n}, \mathbf{n}_\mathrm{P})\mathbf{p} \\
\dot{\boldsymbol{\alpha}} &= -\boldsymbol{\alpha}\bar{\mathbf{F}}^{\mathrm{pc}}(\mathbf{z}_\mathrm{R}, \mathbf{z}_\mathrm{M}, \mathbf{p}, \mathbf{n}, \mathbf{n}_\mathrm{P}) \\
\dot{\mathbf{p}} &= \mathbf{F}(z_\mathrm{M}, \mathbf{z}_\mathrm{R}, \mathbf{z}_\mathrm{M}, \mathbf{p}, \mathbf{n}, \mathbf{n}_\mathrm{P})\mathbf{p} \\
\dot{\mathbf{n}} &= \bar{\mathbf{G}}(\mathbf{z}_\mathrm{R}, \mathbf{z}_\mathrm{M}, \mathbf{p}, \mathbf{n}, \mathbf{n}_\mathrm{P})\mathbf{n} \\
\dot{\mathbf{n}}_\mathrm{P} &= \mathbf{R}(\mathbf{z}_\mathrm{R}, \mathbf{z}_\mathrm{M}, \mathbf{p}, \mathbf{n}, \mathbf{n}_\mathrm{P}),
\end{aligned} \tag{28}$$

where we have for clarity included all the arguments. Next, we write the dynamics of (28) under phenotypic similarity in both fast and slow time, and then obtain two distinct limiting singular equations (by letting δ go to 0) that can be easily analyzed. Finally, we glue them back together by perturbing the obtained singular equations. By doing this the singular system ($\delta = 0$) serves as an approximation to a mutant-resident dynamics under phenotypic similarity (δ small but nonzero) such that all its dynamical properties are preserved.

Let t denote the fast population dynamical time (the original time used throughout this paper) and let τ denote the slow evolutionary time (see also Figure 1). Setting $\tau = \delta t$ we obtain the relation $d\tau = \delta dt$ and then write the mutant-resident dynamics for closely similar phenotypes (δ small but nonzero) either using the original time variable t

$$\begin{aligned}
\frac{\mathrm{d}p_\alpha(t)}{\mathrm{d}t} &= \delta\boldsymbol{\alpha}\frac{\mathrm{d}}{\mathrm{d}\delta}\mathbf{F}^{\mathrm{sel}}(z_\mathrm{M})\Big|_{\delta=0}\mathbf{p} + O(\delta^2) \\
\frac{\mathrm{d}\boldsymbol{\alpha}(t)}{\mathrm{d}t} &= -\boldsymbol{\alpha}(t)\bar{\mathbf{F}}_0^{\mathrm{pc}} + O(\delta) \\
\frac{\mathrm{d}\mathbf{p}(t)}{\mathrm{d}t} &= \bar{\mathbf{F}}_0^{\mathrm{pc}}\mathbf{p}(t) + O(\delta) \\
\frac{\mathrm{d}\mathbf{n}(t)}{\mathrm{d}t} &= \mathbf{H}(z)\mathbf{n}(t) + O(\delta) \\
\frac{\mathrm{d}\mathbf{n}_\mathrm{P}(t)}{\mathrm{d}t} &= \mathbf{P} + O(\delta)
\end{aligned} \tag{29}$$

or using the new time variable τ

$$
\begin{aligned}
\delta\frac{\mathrm{d}p_\alpha(\tau)}{\mathrm{d}\tau} &= \delta\boldsymbol{\alpha}\frac{\mathrm{d}}{\mathrm{d}\delta}\mathbf{F}^{\mathrm{sel}}(z_{\mathrm{M}})\Big|_{\delta=0}\mathbf{p} + O(\delta^2)\\
\delta\frac{\mathrm{d}\boldsymbol{\alpha}(\tau)}{\mathrm{d}\tau} &= -\boldsymbol{\alpha}(\tau)\bar{\mathbf{F}}_0^{\mathrm{pc}} + O(\delta)\\
\delta\frac{\mathrm{d}\mathbf{p}(\tau)}{\mathrm{d}\tau} &= \bar{\mathbf{F}}_0^{\mathrm{pc}}\mathbf{p}(\tau) + O(\delta)\\
\delta\frac{\mathrm{d}\mathbf{n}(\tau)}{\mathrm{d}\tau} &= \mathbf{H}(z)\mathbf{n}(\tau) + O(\delta)\\
\delta\frac{\mathrm{d}\mathbf{n}_{\mathrm{P}}(\tau)}{\mathrm{d}\tau} &= \mathbf{P} + O(\delta).
\end{aligned}
\tag{30}
$$

Since we haven't yet taken any limits the two systems (29) and (30) are identical, the only difference is the notation. Let's now take the limit $\delta \to 0$ and obtain two limiting singular equations, one for fast population dynamical time

$$
\begin{aligned}
\frac{dp_\alpha(t)}{dt} &= 0\\
\frac{d\boldsymbol{\alpha}(t)}{dt} &= -\boldsymbol{\alpha}(t)\bar{\mathbf{F}}_0^{\mathrm{pc}}\\
\frac{d\mathbf{p}(t)}{dt} &= \bar{\mathbf{F}}_0^{\mathrm{pc}}\mathbf{p}(t)\\
\frac{d\mathbf{n}(t)}{dt} &= \mathbf{H}(z)\mathbf{n}(t)\\
\frac{d\mathbf{n}_{\mathrm{P}}(t)}{dt} &= \mathbf{P}
\end{aligned}
\tag{31}
$$

and the second for slow evolutionary time

$$
\begin{aligned}
\frac{dp_\alpha(\tau)}{d\tau} &= \boldsymbol{\alpha}\frac{d}{d\delta}\mathbf{F}^{\mathrm{sel}}(z_{\mathrm{M}})\Big|_{\delta=0}\mathbf{p}\\
0 &= -\boldsymbol{\alpha}(\tau)\bar{\mathbf{F}}_0^{\mathrm{pc}}\\
0 &= \mathbf{F}_0\mathbf{p}(\tau)\\
0 &= \mathbf{H}(z)\mathbf{n}(\tau)\\
0 &= \mathbf{P}.
\end{aligned}
\tag{32}
$$

This confirms that in the fast population dynamical time (31) the average mutant frequency p_α stays constant and that the mutant-resident dynamics reaches the critical manifold $\mathcal{M}_0$ as found in (27), and that the algebraic expression for $\mathcal{M}_0$ can be obtained directly from (32).

Because the variables $\boldsymbol{\alpha}, \mathbf{p}, \mathbf{n}, \mathbf{n}_{\mathrm{P}}$ in (32) have reached their critical manifold $\mathcal{M}_0$, we evaluate the right

hand side of the first line in (32) at the $\mathcal{M}_0$ to obtain

$$\begin{aligned}\left[\boldsymbol{\alpha}\frac{d}{d\delta}\mathbf{F}^{\text{sel}}\Big|_{\delta=0}\mathbf{p}\right]_{\mathcal{M}_0} &= \left[\sum_{a}\alpha_a\sum_{b}\left(\frac{\partial}{\partial z_{\text{M}}}f^{\text{sel}}_{ab}(z_{\text{M}})+\sum_{c}\frac{\partial}{\partial z_{\text{M},c}}f^{\text{sel}}_{ab}(z_{\text{M}})\right)_{\delta=0}p_{\text{M},b}\right]_{\mathcal{M}_0}\\ &= \left[\sum_{a}\alpha_a\sum_{b}\frac{n_b}{n_a}\frac{\partial}{\partial z}h_{ab}(z,\mathbf{z},\mathbf{n},\mathbf{n}_{\text{P}})p_{\text{M},b}(1-p_{\text{M},b})\right]_{\mathcal{M}_0}\\ &= p_\alpha(1-p_\alpha)\sum_{a}\sum_{b}\frac{\hat{\alpha}_a}{\hat{n}_a}\frac{\partial}{\partial z}h_{ab}(z,\mathbf{z},\hat{\mathbf{n}},\hat{\mathbf{n}}_{\text{P}})\hat{n}_b,\end{aligned} \tag{33}$$

where we used (13). Therefore, by defining $\mathbf{v}=(v_a)_{a\in\mathcal{D}}$ as a vector of reproductive values $v_a=\frac{\alpha_a}{n_a}$ of an *individual* in class $a\in\mathcal{D}$ (see Appendix 6.5 for more details), then at $\mathcal{M}_0$ we have

$$\hat{v}_a=\frac{\hat{\alpha}_a}{\hat{n}_a}, \tag{34}$$

and using (33) we can write the slow (singular) mutant-resident evolutionary dynamics (32) with a single equation as

$$\frac{dp_\alpha(\tau)}{d\tau}=p_\alpha(1-p_\alpha)\sum_{a,b}\hat{v}_a\frac{\partial h_{ab}(z)}{\partial z}\hat{n}_b \tag{35}$$

or in a matrix notation as

$$\frac{dp_\alpha(\tau)}{d\tau}=p_\alpha(1-p_\alpha)\hat{\mathbf{v}}\frac{\partial\mathbf{H}(z)}{\partial z}\hat{\mathbf{n}}. \tag{36}$$

Alternatively, one can express (36) in terms of a probability distribution over all classes, i.e. in terms of class frequencies defined as $\pi_a=\frac{n_a}{n},\forall a\in\mathcal{D}$ where $n=\sum_a n_a$ is the total population size. Because $\boldsymbol{\pi}n=\mathbf{n}$, where $\boldsymbol{\pi}=(\pi_a)_{a\in\mathcal{D}}$, one could also scale the individual reproductive values as $\boldsymbol{\nu}=\mathbf{v}n$ (see Appendix 6.5) to get

$$\frac{dp_\alpha(\tau)}{d\tau}=p_\alpha(1-p_\alpha)\hat{\boldsymbol{\nu}}\frac{\partial\mathbf{H}(z)}{\partial z}\hat{\boldsymbol{\pi}}. \tag{37}$$

The two formulations (36) and (37) are equivalent, each providing a different perspective on the same evolutionary process. As the matrix $\mathbf{H}$ gives the *individual* growth-rates, the expression in (36) describes how all (mutant) individuals in different classes contribute to the mutant evolutionary dynamics. In (37), the focus is on an average carrier of the mutant allele and how that representative individual contributes to the mutant dynamics when weighted over all classes the carrier of the mutant can be in. The vector $\hat{\boldsymbol{\pi}}$ thus gives the stationary distribution of classes a mutant, which is sampled from the collection of all mutants (i.e., the mutant lineage), can be in.

Now, whichever formulation (36) or (37) is more convenient, geometric singular perturbation theory guarantees that after initial convergence, the mutant-resident dynamics (29)-(30) in the neighborhood of the manifold $\mathcal{M}_\delta$ is equivalent to (can be approximated by) the dynamics given by the two singular systems (31) and (32) (see Figure 3 and Appendix 6.4). In particular, the dynamics of the weighted

mutant frequency p_α for small but nonzero δ near $\mathcal{M}_\delta$ can be approximated by the dynamics given in (36) and (37) (in Appendix 6.4 the Corollary 3 and the Section 6.4.4). We have thus proved the below "invasion implies substitution"-proposition and its Corollary, given the following assumption holds.

Assumption (A). *Assume that the resident ecological community as defined in* (3) *contains a hyperbolically stable equilibrium* $(\hat{\mathbf{n}}, \hat{\mathbf{n}}_P) \in \mathbb{R}^{m+l}$ *to which the resident population converges to and then stays at.*

Invasion implies substitution-proposition. *Consider an ecological community with a polymorphic demographically (physiologically) structured population as defined in* (3)*, and assume that (A) holds. Suppose that one of the phenotypes in the population undergoes a mutation, and that the mutant phenotype* $z_M \in \mathcal{Z}$ *and its ancestral (resident) phenotype* $z_R \in \mathcal{Z}$ *are closely similar, i.e.* $\delta = z_M - z_R$ *for some small* $\delta \neq 0$*. Then, for sufficiently large time* t *and/or small* δ*, the dynamics of the weighted mutant frequency* p_α *in the resulting mutant-resident ecological community* (28) *can be approximated on the original time scale by*

$$\frac{dp_\alpha(t)}{dt} = \delta p_\alpha(1 - p_\alpha)S(z) + O(\delta^2), \tag{38}$$

where the frequency-independent selection gradient $S(z)$ *can be expressed as*

$$S(z) = \hat{\mathbf{v}} \frac{\partial \mathbf{H}(z, \mathbf{z}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_P)}{\partial z} \hat{\mathbf{n}}, \tag{39a}$$

or alternatively as

$$S(z) = \hat{\boldsymbol{\nu}} \frac{\partial \mathbf{H}(z, \mathbf{z}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_P)}{\partial z} \hat{\boldsymbol{\pi}}. \tag{39b}$$

Successful invasion of a mutant implies the substitution of the resident.

Corollary (C). *The subset of* $\mathcal{Z}$ *where the assumption (A) holds and where the selection gradient* (39) *is nonzero indicates all the possible evolutionary trajectories of the phenotype under selection.*

5 Discussion

We provided a proof of an "invasion implies substitution"-principle and gave a positive answer to all three questions (I)-(III) posed in Section 1 for scalar-valued, polymorphic and well-mixed clonally reproducing populations that are part of a larger ecological community and that are structured into finitely many demographic (or physiological) classes.

The separation of ecology and evolution We proved the "invasion implies substitution"-principle by separating the population dynamical and evolutionary timescales using the weighted average mutant frequency, and then singularly perturbed the mutant-resident dynamics given as ordinary differential equations (Fenichel, 1979; Wiggins, 1994; Jones, 1995; Hek, 2010; Kuehn, 2015; Dercole and Geritz, 2016)

using the phenotypic deviation δ as the perturbation parameter. In this method, which is fully detailed in Appendix 6.4 for the present context, one proceeds in three steps. First, one must be able to write the mutant-resident dynamics for small values of δ in a fast-slow form $\dot{p} = \delta\sigma(p, x, \delta),\ \dot{x} = \varphi(p, x, \delta),$ where p represents a weighted mutant frequency in the population and x should capture all the fast (population dynamical) variables. In Section 3, however, it became apparent that for small δ all dynamical variables are fast variables, including class-specific and mean mutant frequencies, and so the model couldn't readily be written in the above fast-slow form. The solution here was to introduce a new variable which operates purely in slow evolutionary time and is a proxy for the mutant frequency. In Section 3.1 we showed that such a variable is the average mutant frequency weighted by class reproductive values (Taylor, 1990; Leturque and Rousset, 2002; Rousset, 2004; Lehmann and Rousset, 2014; Engen et al., 2014; Lehmann et al., 2016).

Once the mutant-resident dynamics is in the fast-slow form, in the second step one starts analyzing the dynamics of the weighted mutant frequency p. Because studying its dynamics for nonzero δ is a complicated task, one hopes that the dynamics of the much easier model where $\delta = 0$ could serve as an approximation for small but nonzero δ. To achieve this, one must first scale time by using δ as the scaling parameter and then write the mutant-resident dynamics in both fast t and slow time $\tau = \delta t$ while letting δ go to zero. In this step one thus analyzes two singular systems, one in fast time where p is constant and x fluctuates according to $\dot{x} = \varphi(p, x, 0)$, and the other in slow time where x is constant (i.e. is at the steady state) and p fluctuates according to $\frac{d}{d\tau}p = \sigma(p, x, 0)$. For us to be able to draw conclusions from this singular system the variable x must converge to its steady state in fast time. In our model this follows directly from the assumption that the resident steady state $(\hat{\mathbf{n}}, \hat{\mathbf{n}}_{\mathrm{P}})$ is hyperbolically stable, i.e. the real part of all eigenvalues of the Jacobian of the linearized resident dynamics are all negative.

In the third and final step one perturbs the above singular equations by applying geometric singular perturbation results for ordinary differential equations developed in Fenichel (1971, 1974, 1977, 1979). Provided certain conditions are satisfied, one can then equate the dynamics of the singular equations where $\delta = 0$ with the original system where δ is small but nonzero (i.e. the perturbed system). Conveniently, the sufficient condition for such a singular perturbation to be possible is that the steady state is hyperbolic which is true by assumption. Therefore, if invasion implies substitution holds for the singular system, it holds also for the original (perturbed) mutant-resident dynamics whenever the steady state is hyperbolic.

The above-mentioned procedure can be applied to more general (demographically) structured models than the one presented in this paper. First of all, the singular perturbation results in Fenichel (1971, 1974, 1977, 1979) allow a direct generalization of our result to models with attractors other than equilibria, e.g. to limit cycles where population experiences deterministic periodic fluctuations. Because including more complicated attractors would require some amount of additional notions (e.g. time-dependent reproductive values as e.g. discussed in Lion, 2018b) we choose to leave this generalization for future work. Second, more recent but equivalent results on invariant manifolds for semiflows (Bates et al., 1998, 2000; Kuehn, 2015) accommodate a more general demographic (physiological) structure, in particular,

allowing for e.g. continuous age or size distributions. However, calculating the hyperbolicity of steady states is considerably more involved in such cases (Greiner et al., 1994; Gyllenberg, 2007; Kuehn, 2015).

Selection gradient as a map between ecology and evolution The expression for the selection gradient (39) was obtained directly from the timescale separation argument given in Section 4. We found that the selection gradient can indeed be written as conjectured in (2), but with relatedness matrix $\mathbf{R}$ playing no role. This is because we assume infinitely large population sizes with no spatial structure (i.e., a well-mixed population) and hence genealogical relationships between any two individuals do not affect the direction of selection. Nevertheless, the selection gradient can be written solely in terms of resident population dynamical variables and resident growth-rates. This is practical since one can then calculate directly from the resident dynamics which mutations can and cannot fix into the population, that is, one can calculate the fate of the mutation before the mutation actually takes place. In this sense, the selection gradient is a "map" from the ecological to the evolutionary model (see Figure 1).

An analogous selection gradient for large class-structured populations with arbitrary social interactions in a larger ecological community, and thus having the same biological scope, has been previously derived in Lion (2018a,b). The model and the method obtaining the selection gradient however depart from ours in that in Lion (2018a,b) the polymorphism is assumed tightly clustered around its mean and that the dynamical equations were formulated in terms of change in mean phenotype. Such a formulation provides links between the dynamics of the mean trait value and the "invasion implies substitution"-principle and is thus complementary to our approach. The drawback in this approach, however, is that the timescale of dynamical variables such as class-specific mutant frequencies is not easily accessible. Consequently, in particular our results on the critical manifold $\mathcal{M}_0$ (Section 3.2), allows us to confirm that as the class-specific trait variance is proportional to the class-specific mutant frequencies, it is indeed a fast variable approaching the population mean trait variance, a result that was left open in Lion (2018a). We conjecture that the ideas on tightly clustered phenotypes developed in Meszéna et al. (2005) together with the results derived in this paper fully justify the selection gradient presented in Lion (2018a,b).

Long-term evolutionary dynamics The main implication of the "invasion implies substitution"-principle is that it indicates the set of phenotypes that can invade and substitute their ancestral phenotypes, thus providing a tool to study the long-term evolutionary dynamics of the trait under selection (panel C in Figure 1 and Corollary in Section 4). The sequential invasion and substitution can occur whenever the steady state is hyperbolic, thus excluding the possibility of bifurcations that may lead to catastrophic extinctions, and whenever the selection gradient $S(z)$ is nonzero, i.e. as long as we are away from the extrema of the adaptive landscape. Such extrema identify the phenotypic values where invasion no longer implies substitution and where more complicated evolutionary behaviour can occur (Geritz et al., 1998; Priklopil, 2012; Dercole and Geritz, 2016). Nevertheless, because we have formulated our model for arbitrarily polymorphic resident populations, the "invasion implies substitution"-principle holds *whenever* the selection gradient is non-zero (and the steady state is hyperbolic). This is particularly true after evolutionary dynamics converges and escapes a phenotypic value that is a branching point:

"invasion implies substitution"-principle governs the direction of evolution even after the appearance of new morphs.

5.1 Conclusions

This study is part of a quest aiming at generalizing and formalizing the hypothesis that social traits under frequency and/or density dependent selection are generically subject to directional gradual change, whenever mutations cause only small deviations to the phenotype under selection (and in the absence of genetic constraints). Further, directional selection should be quantifiable by a selection gradient that consist of reproductive value and relatedness weighted fitness differentials. In this study this hypothesis was confirmed for well-mixed ecological communities with demographically (physiologically) class-structured populations. Our results are directly applicable to several well-known models, such as SIR-models in epidemiology and stage-structured models in life-history studies, and will be generalized to spatially structured population with limited disperal in a forthcoming study.

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6 Appendix

6.1 Relative growth-rate for arbitrary phenotypes

In the main text, we derived the dynamics for class-specific mutant frequencies (5)-(8), where we obtained a partition for the relative growth-rate matrix for a (single) mutant $\mathbf{F}(z_{\mathrm{M}}) = \mathbf{F}^{\mathrm{sel}}(z_{\mathrm{M}}) + \bar{\mathbf{F}}^{\mathrm{pc}}$, with a term $\bar{\mathbf{F}}^{\mathrm{pc}}$ that is independent of the phenotype of the (single) mutant. Here, we confirm that such a partition exists independently of the phenotype of the individual whose relative growth-rate we are considering by proceeding the same way as in the main text, except that we don't specify the phenotype of the individual whose relative growth-rate we are calculating. That is, we have

$$\begin{aligned}
\dot{p}_{\mathrm{X},a} &= \frac{d}{dt}\left(\frac{n_{\mathrm{X},a}}{n_a}\right) = \frac{\dot{n}_{\mathrm{X},a} n_a - n_{\mathrm{X},a}\dot{n}_a}{n_a^2} \\
&= \frac{1}{n_a}\left[\dot{n}_{\mathrm{X},a} - p_{\mathrm{X},a}\dot{n}_a\right] \\
&= \sum_b \frac{n_b}{n_a} g_{ab}(z_{\mathrm{X}}) p_{\mathrm{X},b} - p_{\mathrm{X},a}\sum_b \frac{n_b}{n_a}\big(g_{ab}(z_{\mathrm{M}})p_{\mathrm{M},a} + g_{ab}(z_{\mathrm{R}})p_{\mathrm{R},a}\big) \\
&= \sum_b \frac{n_b}{n_a} g_{ab}(z_{\mathrm{X}}) p_{\mathrm{X},b} - p_{\mathrm{X},a}\sum_b \frac{n_b}{n_a}\bar{g}_{ab} \\
&= \sum_b \frac{n_b}{n_a} g_{ab}(z_{\mathrm{X}}) p_{\mathrm{X},b} - p_{\mathrm{X},b}\sum_b \frac{n_b}{n_a}\bar{g}_{ab} + p_{\mathrm{X},b}\sum_b \frac{n_b}{n_a}\bar{g}_{ab} - p_{\mathrm{X},a}\sum_b \frac{n_b}{n_a}\bar{g}_{ab} \\
&= \sum_b \frac{n_b}{n_a}\left[g_{ab}(z_{\mathrm{X}}) - \bar{g}_{ab}\right] p_{\mathrm{X},b} + p_{\mathrm{X},b}\sum_{b\neq a}\frac{n_b}{n_a}\bar{g}_{ab} - p_{\mathrm{X},a}\sum_{b\neq a}\frac{n_b}{n_a}\bar{g}_{ab}
\end{aligned} \tag{40}$$

for all $a \in \mathcal{D}$, where $\bar{g}_{ab} = g_{ab}(z_{\mathrm{M}})p_{\mathrm{M},b} + g_{ab}(z_{\mathrm{R}})p_{\mathrm{R},b}$ and $X \in \{\mathrm{M}, \mathrm{R}\}$. Defining $\mathbf{p} := \mathbf{p}_{\mathrm{M}}$ and $\mathbf{1} - \mathbf{p} := \mathbf{p}_{\mathrm{R}}$ as the vector of class-specific mutant and resident frequencies, respectively, we can write

$$\begin{aligned}
\dot{\mathbf{p}}_{\mathrm{X}} &= \mathbf{F}(z_{\mathrm{X}})\mathbf{p}_{\mathrm{X}} \\
&= \left[\bar{\mathbf{F}}^{\mathrm{pc}}(z_{\mathrm{X}}) + \bar{\mathbf{F}}^{\mathrm{pc}}\right]\mathbf{p}_{\mathrm{X}},
\end{aligned} \tag{41}$$

where the entries of $\bar{\mathbf{F}}^{\mathrm{pc}}(z_{\mathrm{X}})$ and $\bar{\mathbf{F}}^{\mathrm{pc}}(z_{\mathrm{X}})$, respectively, are

$$\begin{aligned}
f^{\mathrm{sel}}_{ab}(z_{\mathrm{X}}) &= \frac{n_b}{n_a}\left[g_{ab}(z_{\mathrm{X}}) - \bar{g}_{ab}\right] \\
\bar{f}^{\mathrm{pc}}_{ab} &= \begin{cases} \frac{n_b}{n_a}\bar{g}_{ab} & \forall b \neq a \\ -\sum_{c\neq a}\frac{n_c}{n_a}\bar{g}_{ac}, & \text{for } b = a. \end{cases}
\end{aligned} \tag{42}$$

Notice that the component that gives the rates at which passive changes occur $\bar{\mathbf{F}}^{\mathrm{pc}}$ is the same for both mutant and resident phenotypes. In fact, an analogous expression can be derived for any polymorphism as long as $1 = \sum_{\mathrm{X}} p_{\mathrm{X},a}$ for all $a \in \mathcal{D}$.

6.2 Mean mutant frequency p_{M} and the dynamics of class frequencies

In the main text, we showed that class-specific mutant frequencies $\mathbf{p}$ are both fast population dynamical and slow evolutionary variables. More precisely, we showed that under phenotypic equality ($\delta = 0$) the

dynamics is dominated by the terms of order $O(1)$ (Section 3) and that $\mathbf{p}$ approaches a line of equilibria where $\hat{p}_{\mathrm{M},a} = p$ for all $a \in \mathcal{D}$, after which the dynamics is dominated by the terms of order $O(\delta)$ along this line of equilibria (Section 3.2). Here, we confirm that the same applies for the mean mutant frequency in the total population $p_{\mathrm{M}} = \boldsymbol{\pi}\mathbf{p} = \sum_a \pi_a p_{\mathrm{M},a}$.

To confirm this, it is sufficient to show that $\boldsymbol{\pi}$ approaches in fast population dynamical time an isolated equilibrium which persist under perturbation of δ. If this is so, then the dynamics of p_{M} is first dominated by the terms of order $O(1)$ and then of order $O(\delta)$ and we get our claim. This is checked immediately from the following Section 6.2.1 where we detail the dynamics of class frequencies: because by assumption the steady state $\hat{\mathbf{n}}$ is hyperbolic so is the steady state $\hat{\boldsymbol{\pi}}$ in (51) (and thus it persists under perturbations).

6.2.1 The dynamics in terms of class frequencies

In this section we will re-write the resident dynamics (3) and the relative mutant-resident dynamics (5) in terms of total population densities and class frequencies which are respectively defined as

$$\begin{aligned} n &= \sum_{a \in \mathcal{D}} n_a \\ \pi_a &= \frac{n_a}{n}, \qquad a \in \mathcal{D}. \end{aligned} \tag{43}$$

Note that since n is a scalar we have the relation

$$n\boldsymbol{\pi} = \mathbf{n}. \tag{44}$$

Resident dynamics The dynamics of the total density is obtained by using (43) and by differentiation

$$\dot{n} = \sum_a n_a = \sum_a \sum_b h_{ab}(z) n_b = \sum_a \sum_b h_{ab}(z) \pi_b n = r(z) n \tag{45}$$

where $r(z) := r(z, \mathbf{z}, n, \boldsymbol{\pi}, \mathbf{n}_{\mathrm{P}}) = \sum_a \sum_b h_{ab}(z)\pi_b$ is the total mean growth-rate of an individual in the resident population. The dynamics of class frequencies is obtained by using (43), (45), and by differentiation

$$\dot{\pi}_a = \frac{\dot{n}_a}{n} - \pi_a \frac{\dot{n}}{n} = \sum_b \frac{1}{n} h_{ab}(z) n_b - r(z)\pi_a \quad = \sum_b h_{ab}(z)\pi_b - r(z)\pi_a, \qquad \forall a \in \mathcal{D}, \tag{46}$$

or in a matrix notation

$$\dot{\boldsymbol{\pi}} = (\mathbf{H}(z) - r(z)\mathbb{I})\,\boldsymbol{\pi}, \tag{47}$$

where $\mathbb{I}$ is the identity matrix. We have thus obtained that the resident dynamics (3) can be rewritten as

$$\begin{aligned}
\dot{n} &= r(z)n \\
\dot{\boldsymbol{\pi}} &= (\mathbf{H}(z) - r(z)\mathbb{I})\,\boldsymbol{\pi} \\
\dot{\mathbf{n}}_{\mathrm{P}} &= \mathbf{P}
\end{aligned} \tag{48}$$

Relative mutant-resident dynamics Using (5) and an analogous derivation to the previous section, we obtain for the relative mutant-resident dynamics

$$\begin{aligned}
\dot{\mathbf{p}} &= \mathbf{F}(z_{\mathrm{M}})\mathbf{p} \\
\dot{n} &= \bar{r}n \\
\dot{\boldsymbol{\pi}} &= \left(\bar{\mathbf{G}} - \bar{r}\mathbb{I}\right)\boldsymbol{\pi} \\
\dot{\mathbf{n}}_{\mathrm{P}} &= \mathbf{R}
\end{aligned} \tag{49}$$

where $\bar{r} = \sum_a \sum_b [\bar{g}_{ab}(z_{\mathrm{M}})p_{\mathrm{M},b} + \bar{g}_{ab}p_{\mathrm{R},b}]\pi_b$ is the total mean growth-rate of an individual in the total population. Notice that alternatively $\bar{r} = \sum_a \sum_b [\bar{g}_{ab}(z_{\mathrm{M}})q_{\mathrm{M},b} + \bar{g}_{ab}q_{\mathrm{R},b}]$, where $q_{\mathrm{X},a} = \frac{n_{\mathrm{X},a}}{n}$ is the probability that given an individual is sampled from the total population it is an individual in class $a \in \mathcal{D}$ with phenotype $z_{\mathrm{X}} \in \{z_{\mathrm{M}}, z_{\mathrm{R}}\}$.

Steady state under phenotypic equality In section 3.2, we found that the steady state $\hat{\mathbf{n}} = \hat{\mathbf{n}}_{\mathrm{M}} + \hat{\mathbf{n}}_{\mathrm{R}}$ under phenotypic equality $\delta = 0$ can be solved from

$$\mathbf{0} = \mathbf{H}(z, \mathbf{z}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_{\mathrm{P}})\hat{\mathbf{n}}, \tag{50}$$

and is thus the right eigenvector of the resident matrix $\mathbf{H}(z, \mathbf{z}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_{\mathrm{P}})$ associated with the eigenvalue 0. Here, we are interested to express the steady state under phenotypic equality in terms of the total population size n and class frequencies $\boldsymbol{\pi}$. Using Section 2.3, we have

$$\begin{aligned}
\dot{n} &= \bar{r}\big|_{\delta=0} n = r(z)n \\
\dot{\boldsymbol{\pi}} &= \left(\bar{\mathbf{G}} - \bar{r}\mathbb{I}\right)_{\delta=0}\boldsymbol{\pi} = (\mathbf{H}(z) - r(z)\mathbb{I})\,\boldsymbol{\pi},
\end{aligned} \tag{51}$$

where the (non-trivial) solutions $\hat{n}$ and $\hat{\boldsymbol{\pi}}$ are obtained from

$$\begin{aligned}
0 &= r(z, \mathbf{z}, \hat{n}, \hat{\boldsymbol{\pi}}, \hat{\mathbf{n}}_{\mathrm{P}}) \\
0 &= (\mathbf{H}(z) - r(z, \mathbf{z}, \hat{n}, \hat{\boldsymbol{\pi}}, \hat{\mathbf{n}}_{\mathrm{P}})\mathbb{I})\,\hat{\boldsymbol{\pi}}.
\end{aligned} \tag{52}$$

Using (44) the steady state can be written as

$$(\hat{n}, \hat{\boldsymbol{\pi}}) = (\hat{n}, \frac{\hat{\mathbf{n}}}{\hat{n}}).$$

Note that because $r(z)$ in-front of the identity matrix in (51) is scalar-valued, both $\hat{\mathbf{n}}$ and $\hat{\boldsymbol{\pi}}$ are the right eigenvectors of $\mathbf{H}(z, \mathbf{z}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_{\mathrm{P}})$ associated with the eigenvalue 0 (this is in fact obvious since we have the relation $n\boldsymbol{\pi} = \mathbf{n}$, i.e. an eigenvector scaled by a scalar is also an eigenvector associated with the same eigenvalue).

6.3 Infinite number of equilibria in $\mathcal{M}_0$

Here, we give an argument as to why the singular system $\delta = 0$ contains infinite number of equilibria. Because $\bar{f}^{\mathrm{pc}}_{aa} = -\sum_{b \neq a} \bar{f}^{\mathrm{pc}}_{ab}$ the matrix $\bar{\mathbf{F}}^{\mathrm{pc}}$ is a transition matrix with an eigenvalue 0. Because the eigenvalue is solved from $0 = \det[\bar{\mathbf{F}}^{\mathrm{pc}} - 0 \cdot \mathbb{I}] = \det[\bar{\mathbf{F}}^{\mathrm{pc}}]$, the determinant of $\bar{\mathbf{F}}^{\mathrm{pc}}$ is zero implying that it is not an invertible matrix and hence $\bar{\mathbf{F}}^{\mathrm{pc}}\mathbf{p}$ doesn't have a unique isolated solution $\mathbf{p}$ (see e.g. Hirsch et al., 1974, Proposition on p. 80).

6.4 Fenichel's Theorems

Here, we go through in detail the results of Fenichel (1971, 1974, 1977, 1979) that are relevant for the "invasion implies substitution"-principle. This section can be seen as a general recipe on how to translate any mutant-resident dynamical system (that is expressed in terms of ordinary differential equations) into a singular perturbation problem, and how the theory of Fenichel allows us to obtain a complete description of the dynamics for the mutant frequency in the full mutant-resident model where δ is small but nonzero. We will in most part follow the exposition of Jones (1995); Hek (2010)(with a small dose of Kuehn, 2015).

The full mutant-resident dynamical model (arbitrary δ) as given in (28) is our starting point

$$\begin{aligned}
\dot{p}_\alpha &= \boldsymbol{\alpha}\mathbf{F}^{\mathrm{sel}}(z_{\mathrm{M}}, \mathbf{z}_{\mathrm{R}}, \mathbf{z}_{\mathrm{M}}, \mathbf{p}, \mathbf{n}, \mathbf{n}_{\mathrm{P}})\mathbf{p} \\
\dot{\boldsymbol{\alpha}} &= -\boldsymbol{\alpha}\bar{\mathbf{F}}^{\mathrm{pc}}(\mathbf{z}_{\mathrm{R}}, \mathbf{z}_{\mathrm{M}}, \mathbf{p}, \mathbf{n}, \mathbf{n}_{\mathrm{P}}) \\
\dot{\mathbf{p}} &= \mathbf{F}(z_{\mathrm{M}}, \mathbf{z}_{\mathrm{R}}, \mathbf{z}_{\mathrm{M}}, \mathbf{p}, \mathbf{n}, \mathbf{n}_{\mathrm{P}})\mathbf{p} \\
\dot{\mathbf{n}} &= \bar{\mathbf{G}}(\mathbf{z}_{\mathrm{R}}, \mathbf{z}_{\mathrm{M}}, \mathbf{p}, \mathbf{n}, \mathbf{n}_{\mathrm{P}})\mathbf{n} \\
\dot{\mathbf{n}}_{\mathrm{P}} &= \mathbf{R}(\mathbf{z}_{\mathrm{R}}, \mathbf{z}_{\mathrm{M}}, \mathbf{p}, \mathbf{n}, \mathbf{n}_{\mathrm{P}}).
\end{aligned} \tag{53}$$

This system can be equivalently written as

$$\begin{aligned}
\dot{p}_\alpha &= s(p_\alpha, x, \delta) \\
\dot{x} &= \phi(p_\alpha, x, \delta)
\end{aligned} \tag{54}$$

where $p_\alpha \in [0, 1] \subset \mathbb{R}^1$, $x = (\boldsymbol{\alpha}, \mathbf{p}, \mathbf{n}, \mathbf{n}_{\mathrm{P}}) \in \mathbb{R}^N_+$ (with $N = 3m + l$), and where

$$\begin{aligned}
s(p_\alpha, x, \delta) &= \boldsymbol{\alpha}\mathbf{F}^{\mathrm{sel}}(z_{\mathrm{M}}, \mathbf{z}_{\mathrm{R}}, \mathbf{z}_{\mathrm{M}}, \mathbf{p}, \mathbf{n}, \mathbf{n}_{\mathrm{P}})\mathbf{p} \\
\phi(p_\alpha, x, \delta) &= \left(-\boldsymbol{\alpha}\bar{\mathbf{F}}^{\mathrm{pc}}(\mathbf{z}_{\mathrm{R}}, \mathbf{z}_{\mathrm{M}}, \mathbf{p}, \mathbf{n}, \mathbf{n}_{\mathrm{P}}),\ \mathbf{F}(z_{\mathrm{M}}, \mathbf{z}_{\mathrm{R}}, \mathbf{z}_{\mathrm{M}}, \mathbf{p}, \mathbf{n}, \mathbf{n}_{\mathrm{P}})\mathbf{p},\ \bar{\mathbf{G}}(\mathbf{z}_{\mathrm{R}}, \mathbf{z}_{\mathrm{M}}, \mathbf{p}, \mathbf{n}, \mathbf{n}_{\mathrm{P}})\mathbf{n},\ \mathbf{R}(\mathbf{z}_{\mathrm{R}}, \mathbf{z}_{\mathrm{M}}, \mathbf{p}, \mathbf{n}, \mathbf{n}_{\mathrm{P}})\right).
\end{aligned} \tag{55}$$

(H1) The functions s, ϕ are sufficiently smooth.

Given (H1) the Taylor expansion of (54) about $\delta = 0$ is

$$\begin{aligned} \dot{p}_\alpha &= \delta\sigma(p_\alpha, x, \delta) \\ \dot{x} &= \varphi(p_\alpha, x, \delta), \end{aligned} \tag{56}$$

where

$$\begin{aligned} \sigma(p_\alpha, x, \delta) &= \frac{\mathrm{d}}{\mathrm{d}\delta} s(p_\alpha, x, \delta)\Big|_{\delta=0} + O(\delta) \\ \varphi(p_\alpha, x, \delta) &= \phi(p_\alpha, x, 0) + \delta \frac{\mathrm{d}}{\mathrm{d}\delta} \phi(p_\alpha, x, \delta)\Big|_{\delta=0} + O(\delta^2). \end{aligned} \tag{57}$$

6.4.1 The relative mutant-resident dynamics

As in the main text, let t be the fast (population dynamical) time and $\tau = \delta t$ the slow (evolutionary) time. For simplicity we will use a dot for the time derivative in fast time (as in the main text) and a comma for the time-derivative in slow time.

The original (perturbed) fast and slow system We can write, for small but nonzero δ, the system (56) in both fast and slow time as

$$\begin{aligned} \dot{p}_\alpha &= \delta\sigma(p_\alpha, x, \delta) \\ \dot{x} &= \varphi(p_\alpha, x, \delta), \end{aligned} \tag{58}$$

and

$$\begin{aligned} p'_\alpha &= \sigma(p_\alpha, x, \delta) \\ \delta x' &= \varphi(p_\alpha, x, \delta), \end{aligned} \tag{59}$$

together with (57), and we re-iterate that $p_\alpha \in [0, 1] \subset \mathbb{R}^1$ and $x \in \mathbb{R}^N_+$ (with $N = 3m + l$).

The singular fast and slow system By taking the limit $\delta \to 0$ and by applying (57) we obtain two singular sets of equations for both fast and slow time:

$$\begin{aligned} \dot{p}_\alpha &= 0 \\ \dot{x} &= \varphi(p_\alpha, x, 0) = \phi(p_\alpha, x, 0) \end{aligned} \tag{60}$$

and

$$\begin{aligned} p'_\alpha &= \sigma(p_\alpha, x, 0) = \frac{\mathrm{d}}{\mathrm{d}\delta} s(p_\alpha, x, \delta)\Big|_{\delta=0} \\ 0 &= \varphi(p_\alpha, x, 0) = \phi(p_\alpha, x, 0). \end{aligned} \tag{61}$$

6.4.2 Fenichel's Theorems 1 and 2

Throughout, whenever we are referring to a distance between two nonempty sets we use the notion of Hausdorff distance (see e.g. Kuehn, 2015, p. 55).

Critical manifold The set of critical (equilibrium) points $\varphi(p_\alpha, x, 0) = 0$ is obtained by solving N equations yielding an 1-dimensional manifold. That is, the set of critical (equilibrium) points is parametrized by p_α. We will denote a (biologically relevant) subset of those points with

$$\mathcal{M}_0 \subset \{ \ (p_\alpha, x) \mid \varphi(p_\alpha, x, 0) = 0 \ \}, \tag{62}$$

which is the critical manifold mentioned in the main text. The manifold $\mathcal{M}_0$ is normally hyperbolic because (by assumption) the linearization of (58) at each point in $\mathcal{M}_0$ has exactly one eigenvalue on the imaginary axis (Jones, 1995, Definition 1, p. 49). This means that the dynamics in the neighborhood of this manifold is governed by the non-zero eigenvalues and the flow on the manifold is governed by the zero eigenvalue, i.e. the dynamics on the manifold is neutral (each point is mapped to itself). Note also that since $[0, 1]$ is compact the following hypothesis holds throughout.

(H2) The set $\mathcal{M}_0$ is compact and normally hyperbolic. Moreover, the linearization of (58) at each point in $\mathcal{M}_0$ has exactly one eigenvalue on the imaginary axis and N eigenvalues on the left-side of the imaginary axis (i.e. the manifold $\mathcal{M}_0$ is locally asymptotically stable).

The following theorem is an adaptation from Jones (1995, Theorem 1, p. 49) and Hek (2010, Theorem 2, p. 354).

Fenichel's Invariant Manifold Theorem 1. *Assuming (H1) and (H2), for δ non-zero but sufficiently small, there exists a (slow) manifold $\mathcal{M}_\delta$ that lies within $O(\delta)$ of $\mathcal{M}_0$ and is diffeomorphic to $\mathcal{M}_0$. Moreover, it is invariant under the flow of* (58).

Remarks: i) Diffeomorphism guarantees that (58) restricted to $\mathcal{M}_\delta$ is a small perturbation away from (61) (Hek, 2010, see the final paragraph on p. 354); ii) This theorem has been also given in Hirsch et al. (1977). iii) Note that at the moment we only know about the flow on the manifold $\mathcal{M}_\delta$ and not in the neighborhood of the manifold (which will be addressed in the following theorem). iv) Jones (1995) uses the concept of local invariance. This concept, however, is not needed in our model because our critical manifold has a boundary which can't be crossed by any trajectory (Jones, 1995, see the final paragraph on p. 49): the two boundaries of $\mathcal{M}_0$ are $p_\alpha = 0$ and $p_\alpha = 1$ which are always (for any model and for any parameter values) invariant.

The following version of the theorem is an adaptation from (Jones, 1995, Theorem 3, p. 62) and (Hek, 2010, Theorem 4, p. 359).

Fenichel's Invariant Manifold Theorem 2. *Assuming (H1) and (H2), for δ non-zero but sufficiently small, there exists a stable manifold $W^s(\mathcal{M}_\delta)$ that is diffeomorphic to and lies within $O(\delta)$ of $W^s(\mathcal{M}_0)$. Moreover, $W^s(\mathcal{M}_\delta)$ is invariant under the flow of* (58).

Remarks: i) The stable manifolds $W^s(\mathcal{M}_0)$ and $W^s(\mathcal{M}_\delta)$ are $N+1$-dimensional. ii) The solutions in $W^s(\mathcal{M}_\delta)$ decay to $\mathcal{M}_\delta$ at an exponential rate (see the next theorem and corollaries), but not to any specific point. iii) The above theorem holds when we are in a sufficiently close neighborhood of $\mathcal{M}_\delta$ (this is being dealt with in Section 6.4.3).

6.4.3 Fenichel's Theorem 3 and its Corollaries

In this section we will discuss the relative mutant-resident dynamics in the neighborhood D of $\mathcal{M}_\delta$ (and hence in the neighborhood of $\mathcal{M}_0$). A normally hyperbolic critical manifold $\mathcal{M}_0$, by definition, consists of critical points y_0 (where $y = (p_\alpha, x)$ and the subscript 0 denotes that the point y is in $\mathcal{M}_0$), each of which has its own stable manifold $W^s(y_0)$, which is N-dimensional (Hek, 2010, p. 372, Section 6). We thus have

$$W^s(\mathcal{M}_0) = \cup_{y_0 \in \mathcal{M}_0} W^s(y_0). \tag{63}$$

The point $y_0 \in \mathcal{M}_0$ is called a *base point* and the manifolds $W^s(y_0)$ are *fibers* of $W^s(\mathcal{M}_0)$. Note that in the previous Theorem 2 we saw that $W^s(\mathcal{M}_0)$ perturbs to $W^s(\mathcal{M}_\delta)$. The question is whether $W^s(y_0)$ also perturbs to an analogues object. This is not obvious because whereas the point y_0 is invariant and so is $W^s(y_0)$, its counterpart $W^s(y_\delta)$ for $y_\delta \in \mathcal{M}_\delta$ is not invariant and so isn't y_δ (cause y_δ in general isn't an equilibrium). However, as discussed in Hek (2010, second and third paragraph on p. 376, Section 6.1.), the whole family $W^s(\mathcal{M}_\delta)$ is invariant in the sense of the following theorems and corollaries.

Let's restrict our attention to the neighborhood D of $\mathcal{M}_\delta$, where we can safely assume that the linear terms (eigenvalues) of (58) dominate the dynamics. Lets focus on the trajectories in $W^s(\mathcal{M}_\delta)$ that are in the neighborhood D. Let $y \cdot t$ denote the application of a flow after time t to an initial point y. Similarly, $A \cdot t$ denotes the application of the flow after time t to a set A, and $y \cdot [t_1, t_2]$ is the resulting trajectory if the flow is applied over the interval $[t_1, t_2]$ (Hek, 2010, Section 6.1.).

The following definition is an adaptation from Hek (2010, Definition on p. 376) and Jones (1995, Definition 3 on p. 74).

Definition The forward evolution of a set $A \subset D$ restricted to D is given by the set

$$A \cdot_D t = \{y \cdot t \mid y \in A \text{ and } y \cdot [0, t] \subset D\}. \tag{64}$$

The following version of the theorem is an adaptation from Jones (1995, Theorem 6, p. 74) and Hek (2010, Theorem 8, p. 376 and Figures in Section 6.1.).

Fenichel's Invariant Manifold Theorem 3. *Assume (H1)-(H2). For every $y_\delta \in \mathcal{M}_\delta$, there is an N-dimensional manifold*

$$W^s(y_\delta) \subset W^s(\mathcal{M}_\delta) \tag{65}$$

that is $O(\delta)$ close and diffeomorphic to $W^s(y_0)$. The family $\{W^s(y_\delta) \mid y_\delta \in \mathcal{M}_\delta\}$ is invariant in the sense that

$$W^s(y_\delta) \cdot_D t \subset W^s(y_\delta \cdot t) \tag{66}$$

if $y_\delta \cdot r \in D$ for all $r \in [0, t]$.

Remark: This somewhat abstract theorem is nicely depicted in a diagram in Hek (2010, p. 377).

The following version of the corollary is an adaptation from Jones (1995, Corollary 1, p. 76) and Hek (2010, Corollary 9, p. 377).

Corollary 1. *There are constants $\kappa, \beta > 0$ so that if $y \in W^s(y_\delta) \cap D$, then*

$$||y \cdot t - y_\delta \cdot t|| \leq \kappa \exp[-\beta t] \tag{67}$$

for all $t \geq 0$ for which $y \cdot [0, t] \subset D$ and $y_\delta \cdot [0, t] \subset \mathcal{M}_\delta$.

The following corollary immediately follows (Hek, 2010, see the discussion after Corollary 9, p. 378):

Corollary 2. *Suppose that $y \in W^s(\mathcal{M}_\delta)$ has a base point $y_\delta \in \mathcal{M}_\delta$, then*

$$||y \cdot t^* - y_\delta \cdot t^*|| \leq C\delta, \qquad \forall t^* \geq \beta^{-1} \log \frac{\kappa}{C\delta}. \tag{68}$$

This means that we can find a point in time t^* after which the distance between any two points, one point on $\mathcal{M}_\delta$ and the other in the neighborhood D, is of distance $O(\delta)$. Note the resemblance of this inequality to Nagylaki (1979, equation (37) on p. 440).

Finally, the following Corollary 3 is central in equating the mutant-relative dynamics for small non-zero δ in fast (original) time t to the dynamics obtained for the singular system in fast time τ. This follows from the previous Corollaries 1 and 2 by realizing that instead of talking about forward evolution of points we may talk directly about trajectories (Hek, 2010, see the final paragraph of Section 6.1.):

Corollary 3. *Associated to a trajectory $\gamma(t; y) \subset W^s(\mathcal{M}_\delta)$, there is trajectory $\gamma_\delta(t; y_\delta) \subset \mathcal{M}_\delta$, with $\gamma(0; y) = y$ and $\gamma_\delta(0; y_\delta) = y_\delta$, such that*

$$||\gamma(t; y) - \gamma_\delta(t; y_\delta)|| \leq C\delta, \qquad \forall t \geq \beta^{-1} \log \frac{\kappa}{C\delta}. \tag{69}$$

Remark: This Corollary gives the justification for the bottom right panel of Figure 3: the trajectory $\gamma_\delta(t; y_\delta)$ is the trajectory on the slow manifold $\mathcal{M}_\delta$, and the trajectory $\gamma(t; y)$ is the one in the neighborhood of $\mathcal{M}_\delta$ that is approaching $\mathcal{M}_\delta$ and the trajectory $\gamma_\delta(t; y_\delta)$.

6.4.4 Relating the slow-time singular system (36)-(37) to Equation (1)

From Theorem 1, we obtained that $\mathcal{M}_\delta$ and $\mathcal{M}_0$ are $O(\delta)$-distance away, that is, with some abuse of notation, we got

$$y_\delta = y_0 + O(\delta), \tag{70}$$

which in the model (53) reads as

$$\begin{aligned} &\hat{\mathbf{n}}_\delta = \hat{\mathbf{n}}_0 + O(\delta), \qquad \hat{\mathbf{n}}_{\mathrm{P},\delta} = \hat{\mathbf{n}}_{\mathrm{P},0} + O(\delta), \qquad \hat{\boldsymbol{\alpha}}_\delta \quad = \hat{\boldsymbol{\alpha}}_0 + O(\delta) \\ &\hat{\mathbf{p}}_\delta = \hat{\mathbf{p}}_0 + O(\delta), \quad \text{where} \quad \hat{\mathbf{p}} = (p, \ldots, p) \\ &p_{\alpha,\delta} = \hat{\boldsymbol{\alpha}}_0 \hat{\mathbf{p}}_0 + O(\delta). \end{aligned} \tag{71}$$

Here, the subscript δ and 0 denote that those variables take values on $\mathcal{M}_\delta$ and $\mathcal{M}_0$, respectively. Then, using Corollary 2, we have that the estimates (70) and (71) hold $\forall t \geq \beta^{-1} \log \frac{\kappa}{C\delta}$, i.e.

$$y_D = y_0 + O(\delta), \tag{72}$$

which in the model (53) reads as

$$\begin{aligned} &\hat{\mathbf{n}}_D = \hat{\mathbf{n}}_0 + O(\delta), \qquad \hat{\mathbf{n}}_{\mathrm{P},D} = \hat{\mathbf{n}}_{\mathrm{P},0} + O(\delta), \qquad \hat{\boldsymbol{\alpha}}_D \quad = \hat{\boldsymbol{\alpha}}_D + O(\delta) \\ &\hat{\mathbf{p}}_D = \hat{\mathbf{p}}_0 + O(\delta), \quad \text{where} \quad \hat{\mathbf{p}}_0 = (p, \ldots, p) \\ &p_{\alpha,D} = \boldsymbol{\alpha}_0 \hat{\mathbf{p}}_0 + O(\delta), \end{aligned} \tag{73}$$

$\forall t \geq \beta^{-1} \log \frac{\kappa}{C\delta}$, where we use the subscript D to denote that y takes a value in D. Moreover, by Taylor expansion we also have $\forall t \geq \beta^{-1} \log \frac{\kappa}{C\delta}$ that

$$\frac{\partial \mathbf{H}(z)}{\partial z}\Big|_D = \frac{\partial \mathbf{H}(z)}{\partial z}\Big|_{\mathcal{M}_0} + O(\delta). \tag{74}$$

Now, in the main text (36) (or alternatively (37)) we derived for the slow singular system $\delta = 0$ an equation

$$p'_\alpha = p_\alpha(1 - p_\alpha)\hat{\mathbf{v}} \frac{\partial \mathbf{H}}{\partial z} \hat{\mathbf{n}}, \tag{75}$$

and by using (72)-(74) and the Corollary 3 we have that p_α in the neighborhood D of $\mathcal{M}_\delta$ can be written in slow evolutionary time τ as

$$p'_\alpha = p_\alpha(1 - p_\alpha)\hat{\mathbf{v}} \frac{\partial \mathbf{H}}{\partial z} \hat{\mathbf{n}} + O(\delta) \tag{76}$$

and therefore in fast original time t as

$$\dot{p}_\alpha = \delta p_\alpha(1 - p_\alpha)\hat{\mathbf{v}} \frac{\partial \mathbf{H}}{\partial z} \hat{\mathbf{n}} + O(\delta^2), \tag{77}$$

whenever $t \geq \beta^{-1} \log \frac{\kappa}{C\delta}$ (which can also be written in terms of τ). This gives a full justification to equation (1) in the main text.

6.5 Individual reproductive values

This exposition in this Appendix is motivated by Lion (2018b) who, in contrast to standard practice in calculating the reproductive values only at the steady state, defined the reproductive values in both fast population dynamical as well as slow evolutionary time. We, however, depart from the exposition of Lion (2018b) by deriving a dynamical equation (analogues to the one in Lion (2018b)) for an alternatively scaled definition for individual reproductive value. Moreover, in the final Section 6.5.4 we show an alternative derivation for the dynamics of the weighted mutant frequency p_α by using such individual reproductive values.

In e.g., Taylor (1990); Rousset and Ronce (2004); Lion (2018b) the individual reproductive values are defined as

$$\nu_a = \frac{\alpha_a}{\pi_a}, \qquad \forall a \in \mathcal{D}; \tag{78a}$$

namely, such that they satisfy the normalization

$$\boldsymbol{\nu} \cdot \boldsymbol{\pi} = \sum_a \nu_a \pi_a = 1. \tag{78b}$$

(recall that$\sum_a \alpha_a = 1$). Here, we also use the following definition

$$v_a = \frac{\alpha_a}{n_a}, \qquad \forall a \in \mathcal{D}, \tag{78c}$$

and owing to $\nu_a \pi_a = v_a n_a, \forall a \in \mathcal{D}$, we have

$$\begin{aligned} \boldsymbol{\nu} \cdot \boldsymbol{\pi} &= \sum_a \nu_a \pi_a = 1 \\ \mathbf{v} \cdot \mathbf{n} &= \sum_a v_a n_a = 1, \end{aligned} \tag{79}$$

where $\boldsymbol{\nu}, \mathbf{v}$ are the vectors of ν_a and v_a, respectively. Also, recall that $\pi_a n = n_a$ and hence

$$\begin{aligned} \boldsymbol{\pi} n &= \mathbf{n} \\ \boldsymbol{\nu} &= \mathbf{v} n. \end{aligned} \tag{80}$$

6.5.1 The dynamics of v_a

By differentiation we obtain

$$\begin{aligned}
\dot{v}_a &= \frac{1}{n_a}\dot{\alpha}_a - \frac{1}{n_a}v_a\dot{n}_a \\
&= -\frac{1}{n_a}\left[\sum_{\mathscr{b}}\alpha_{\mathscr{b}}\frac{n_a}{n_{\mathscr{b}}}\bar{g}_{\mathscr{b}a} - \alpha_a\sum_{\mathscr{b}}\frac{n_{\mathscr{b}}}{n_a}\bar{g}_{a\mathscr{b}}\right] - \frac{1}{n_a}v_a\sum_{\mathscr{b}}\bar{g}_{a\mathscr{b}}n_{\mathscr{b}} \\
&= -\sum_{\mathscr{b}}v_{\mathscr{b}}\bar{g}_{\mathscr{b}a} + v_a\sum_{\mathscr{b}}\frac{n_{\mathscr{b}}}{n_a}\bar{g}_{a\mathscr{b}} - v_a\sum_{\mathscr{b}}\frac{n_{\mathscr{b}}}{n_a}\bar{g}_{a\mathscr{b}} \\
&= -\sum_{\mathscr{b}}v_{\mathscr{b}}\bar{g}_{\mathscr{b}a},, \qquad \forall \boldsymbol{a} \in \mathcal{D},
\end{aligned} \tag{81}$$

which can be expressed with a matrix notation as

$$\dot{\mathbf{v}} = -\mathbf{v}\bar{\mathbf{G}}. \tag{82}$$

6.5.2 The dynamics of ν_a

Using (8), Section 6.2.1, and performing a similar calculation to above, we obtain

$$\begin{aligned}
\dot{\nu}_a &= \frac{1}{\pi_a}\dot{\alpha}_a - \nu_a\frac{1}{\pi_a}\dot{\pi}_a \\
&= \left[-\sum_{\mathscr{b}}\frac{\alpha_{\mathscr{b}}}{\pi_a}\frac{n_a}{n_{\mathscr{b}}}\bar{g}_{\mathscr{b}a} + \frac{\alpha_a}{\pi_a}\sum_{\mathscr{b}}\frac{n_{\mathscr{b}}}{n_a}\bar{g}_{a\mathscr{b}}\right] - \frac{\nu_a}{\pi_a}\left[\sum_{\mathscr{b}}\bar{g}_{a\mathscr{b}}\pi_{\mathscr{b}} - \bar{r}\pi_a\right] \\
&= -\sum_{\mathscr{b}}\nu_{\mathscr{b}}\bar{g}_{\mathscr{b}a} + \nu_a\bar{r}
\end{aligned} \tag{83}$$

which can be expressed with a matrix notation as

$$\dot{\boldsymbol{\nu}} = -\boldsymbol{\nu}\left(\bar{\mathbf{G}} - \bar{r}\mathbb{I}\right). \tag{84}$$

6.5.3 Individual reproductive values v_a and ν_a as left eigenvectors

Using (82) and Section 2.3 the slow evolutionary time definition of $\mathbf{v}$ under phenotypic equality $\delta = 0$ is

$$\mathbf{0} = \hat{\mathbf{v}}\mathbf{H}(z, \mathbf{z}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_{\mathrm{P}}), \tag{85}$$

that is, $\hat{\mathbf{v}}$ is the left eigenvector of the resident matrix $\mathbf{H}(z, \mathbf{z}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_{\mathrm{P}})$ associated with the eigenvalue 0. Similarly, the slow evolutionary time definition of $\boldsymbol{\nu}$ under phenotypic equality $\delta = 0$ is

$$\mathbf{0} = \hat{\boldsymbol{\nu}}\left(\mathbf{H}(z, \mathbf{z}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_{\mathrm{P}}) - r\mathbb{I}\right), \tag{86}$$

and because the identity matrix is multiplied by a scalar, the solution to above is equivalent to solving

$$\mathbf{0} = \hat{\boldsymbol{\nu}}\mathbf{H}(z, \mathbf{z}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_{\mathrm{P}}), \tag{87}$$

hence both $\hat{\boldsymbol{\nu}}$ and $\hat{\mathbf{v}}$ are the left eigenvectors of the resident matrix $\mathbf{H}(z, \mathbf{z}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_{\mathrm{P}})$ associated with the eigenvalue 0. Moreover, from (80) we have

$$\hat{\boldsymbol{\nu}} = \hat{n}\hat{\mathbf{v}}. \tag{88}$$

6.5.4 The dynamics of the weighted mutant frequency using individual reproductive values

Here we show a more direct calculation for the dynamics of the weighted mutant frequency p_α. Because

$$\boldsymbol{\alpha}\mathbf{p} = \sum_a \alpha_a \frac{n_{\mathrm{M},a}}{n_a} = \sum_a v_a n_{\mathrm{M},a} = \mathbf{v}\mathbf{n}_{\mathrm{M}} \tag{89}$$

we have

$$p_\alpha = \boldsymbol{\alpha}\mathbf{p} = \mathbf{v}\mathbf{n}_{\mathrm{M}} = p_v. \tag{90}$$

Therefore

$$\begin{aligned} \dot{p}_v &= \dot{\mathbf{v}}\mathbf{n}_{\mathrm{M}} + \mathbf{v}\dot{\mathbf{n}}_{\mathrm{M}} \\ &= \dot{\mathbf{v}}\mathbf{n}_{\mathrm{M}} + \mathbf{v}\mathbf{G}(z_{\mathrm{M}})\mathbf{n}_{\mathrm{M}}, \end{aligned} \tag{91}$$

where $\mathbf{G}(z_{\mathrm{M}})$ can be partitioned as

$$\mathbf{G}(z_{\mathrm{M}}) = \mathbf{G}^{\mathrm{sel}}(z_{\mathrm{M}}) + \bar{\mathbf{G}}, \tag{92}$$

where $\mathbf{G}^{\mathrm{sel}}(z_{\mathrm{M}}) = (g^{\mathrm{sel}}_{ab})_{a,b\in\mathcal{D}}$ and

$$g^{\mathrm{sel}}_{ab} = g_{ab}(z_{\mathrm{M}}) - \bar{g}_{ab}, \qquad \forall a, a \in \mathcal{D}, \tag{93}$$

and $\bar{\mathbf{G}}$ is as in the main text (5). The weighted mutant frequency can thus be written directly in terms of individual reproductive values as

$$\dot{p}_v = \left[\dot{\mathbf{v}} + \mathbf{v}\bar{\mathbf{G}}\right]\mathbf{n}_{\mathrm{M}} + \mathbf{v}\mathbf{G}^{\mathrm{sel}}\mathbf{n}_{\mathrm{M}}, \tag{94}$$

and by defining $\mathbf{v}$ such that it satisfies (82) we get

$$\dot{p}_v = \mathbf{v}\mathbf{G}^{\mathrm{sel}}\mathbf{n}_{\mathrm{M}}. \tag{95}$$

Notice that this is indeed equivalent to (19) and that under phenotypic equality $\dot{p}_v|_{\delta=0} = 0$. Now, taking the derivative of the above with respect to δ and using Section 2.3 we immediately obtain (36).