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. This states that 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 it unsettled in precisely which models does the "invasion implies substitution"-principle really hold. 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. 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. We do this by setting up a continuous-time mutant-resident dynamical system for several interacting populations and species, and derive a closed expression for the selection gradient by separating the population dynamical and evolutionary timescales using geometric singular perturbation methods. We show that the selection gradient is constant in the relevant timescale and that it depends only on the resident phenotype, individual growth-rates, equilibrium population densities and reproductive values, all of which are calculated from the resident dynamics. Furthermore, we relate our results to previous work and discuss the theoretical tools required to address such problems. Our work contributes to the theoretical foundations of evolutionary ecology.

1   Introduction

A central theme in evolutionary biology is to understand long-term evolution; 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 [15, 48]. 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 not much can be said about the evolutionary adaptive trajectory of social traits in general.

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 [30, 14, 45, 24, 53, 38, 51, 54, 23, 52, 8, 12, 37]. Such a paradigmatic Darwinian process (e.g., [5]) relies on the ”invasion implies substitution”-principle, which is the ultimate fixation in the population of any mutant being favored by selection when initially rare in the population. 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 [51, 23, 12, 37] and has been called a "gift from God" [29].

The intuitive argument for justifying ”invasion implies substitution”-principle can be made by considering a well-mixed haploid population in discrete time (no overlapping generation or further division in class structure) with only two alleles, a wild-type (resident) allele coding for some phenotype and a mutant allele coding for some closely similar phenotype. The argument is that the dynamics of the frequency of the mutant allele 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). 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 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 a frequency-dependent but always positive measure of genetic variation at the loci under selection, e.g., for a well-mixed population this is simply $p(1-p)$. 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
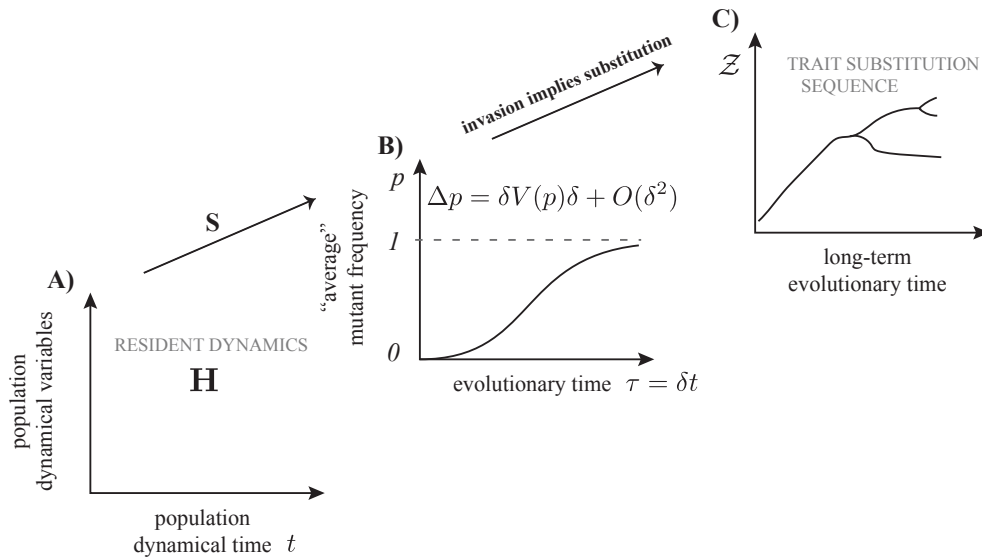
Figure 1: The three timescales that are relevant for the "invasion implies substitution"-principle. A) The population dynamical timescale at which all fast genetic and demographic (ecological) dynamical variables converge to their steady state B) The evolutionary timescale at which the (average) mutant frequency p changes, and where mutant phenotype may or may not substitute its ancestral resident phenotype. At this timescale 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 [46]). This panel gives the timescale of the trait substitution sequence where each individual trait substitution is defined as an invasion implies substitution event.

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, may brake down in more 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 [38, 54, 52]. Indeed, class-specific mutant frequencies and thus also the mean mutant frequency in the population are usually not purely slow evolutionary variables [38, 54]. Moreover, when individuals are structured into continuous or countably infinite age-classes and habitats [44, 11, 10, 52], population dynamical variables such as population densities or genetic associations are not necessarily fast either [26, 52, 27]. 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 with vector-valued traits and with finite number of demographic and spatial classes [51, 12, 43]. The central step here follows from the realization that when the mutant frequency in the population p is re-defined as the average frequency weighted by class-specific reproductive values [58, 51, 37, 25, 39, 41], 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
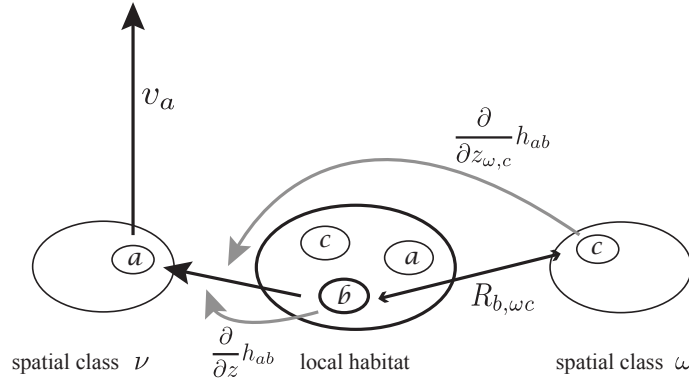
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Figure 2: The partitioning of the selection gradient S. Suppose the fraction of mutant individuals in the total population is p, and as a thought experiment, suppose that before a "switch" is turned on the deviation between the mutant and resident phenotype δ is zero. Selection gradient can then be seen as a measure of how much the relative mutant production (relative to the resident) changes when the switch is turned on and δ becomes nonzero. Now, suppose that the switch is off ($\delta = 0$) and suppose that a single mutant individual in demographic class $b \in \mathcal{D}$ that resides in some discrete spatial location (denoted as "local habitat") is producing (mutant) individuals into $a \in \mathcal{D}$ with a rate h_{ab}. Turning the switch on can affect the relative production of (mutant) individuals in two ways. It can affect the production "directly" because the individual in $b \in \mathcal{D}$ has the mutation $\frac{\partial}{\partial z_{\text{self}}} h_{ab}$, and, it can also be affected "indirectly" due to social (frequency or density dependent) interactions with other mutant individuals, $\frac{\partial h_{ab}}{\partial z_{\text{others in } \omega, c}}$, multiplied by the probability that individuals in ω, c also have the mutation (which is conditional on the individual in $b \in \mathcal{D}$), 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 $a \in \mathcal{D}$ 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.

according to the following generic form

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

Here, the matrix $\mathbf{H}$ is a resident growth-rate matrix whose elements h_{ab} give the rates at which individuals are produced into a demographic class $a \in \mathcal{D}$ by a single resident individual in a demographic class $b \in \mathcal{D}$ 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). The partial derivatives $\frac{\partial \mathbf{H}}{\partial z_{\text{self}}}$ and $\frac{\partial \mathbf{H}}{\partial z_{\text{others in } \omega, c}}$ are defined according to the trait space $\mathcal{Z}$ under consideration, and are taken with respect to 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 $\omega \in \mathcal{G}, c \in \mathcal{D}$, 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 $\mathbf{R}_{\text{others in } \omega, c}$ 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 $c \in \mathcal{D}$. That is, the elements of $\mathbf{R}_{\text{others in } \omega, c}$ are neutral relatedness coefficients [51]. To our knowledge, no generalizations of (2) to more generally structured populations are known.

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Equation (2) is consistent with all previous work on the "invasion implies substitution"-principle. In particular, two categories of demographically unstructured population models have rigorously treated the "invasion implies substitution"-principle. The first category are well-mixed (panmictic) population models with fluctuating demography caused by density and frequency-dependent selection [23, 42, 8, 7], where the single population dynamical variable is the total population density. These models include scalar-valued [8, 7] and vector-valued traits [23, 42], arbitrary [8] or tightly clustered polymorphisms [42], as well as populations that are part of a larger ecological community [8]. The "invasion implies substitution"-principle was here proven by singularly perturbing [21, 31] 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 [8, 7]. Such perturbation analysis is essential in situations where population dynamical variables (here population density) may not persist under perturbations caused by the invasion of a mutant phenotype [22] and may lead e.g. to a catastrophic extinction of the population [28, 47]. The selection gradient was then shown to take the form $S = \frac{\partial h}{\partial z_{\text{self}}}$ [42, 8, 7], where population density comes into play as an argument of the growth-rate function.

The second category of demographically unstructured models [63, 59, 55, 60, 51, 52] assumes that the population exhibits spatial or group structure with limited dispersal, but as the population experiences no 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 using a diffusion approximation method for two timescales [16, 17] 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 relatedness which in this model is density-independent, the obtained results hold also for small but nonzero phenotypic deviations and hence the above-mentioned perturbation analysis is not required. This method was applied in the island model of dispersal for the discrete-time Wright-Fisher model [59] and for the Moran model [60], whereas [55, 51, 52] 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 $S = \frac{\partial h}{\partial z_{\text{self}}} + \frac{\partial h}{\partial z_{\text{others}}} R_{\text{others}}$ [55, 51, 52]. A related model considers isolation by distance [52]. 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 [56]. 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 (genealogical association) 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, [40, 39] discuss 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, and where its dynamics is formulated in terms of the Price equation. 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 in this model takes form $S = \mathbf{v}\frac{\partial \mathbf{H}}{\partial z_{\mathrm{self}}}\mathbf{n}$. Second, the "invasion implies substitution"-principle has been considered in an island model of dispersal with finite but demographically fluctuating local population sizes [51, 54, 36] and with a further division into demographic classes such as age or size classes [51]. 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 [58, 38, 51] and using the timescale separation arguments of [16, 17], in which case the selection gradient can be expressed under the form $S = \mathbf{v}\left[\frac{\partial \mathbf{H}}{\partial z_{\mathrm{self}}} + \frac{\partial \mathbf{H}}{\partial z_{\mathrm{others}}}\mathbf{R}_{\mathrm{other}}\right]\mathbf{n}$ [51, 36]. Similarly to the spatially structured model without demographic fluctuations, the model contains only one spatial location and so relatedness only needs to be calculated within groups that belong to the same demographic and spatial class (notice no summation in the selection gradient). However, because each group consists of individuals that fluctuate between different demographic classes the growth-rate functions as well as the relatedness are density-dependent, requiring further 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 specified and detailed proof for the case for 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 $\mathcal{Z}, \mathcal{D}, \mathcal{G}$?

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

(III) If 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 the resident growth-rate matrix (operator) $\mathbf{H}$ 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 quantitative trait under selection in a well-mixed population structured

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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 that we apply to limited dispersal in a subsequent paper. We also formulate our model in continuous-time and from the outset assume that the population size is large. In this sense our treatment complements previous well-mixed demographically class-structured models (in particular those in [51]) where one usually starts with a discrete-time and finite total population size formulation and then by using some form of timescale separation argument scales time and system size, while letting phenotypic deviation between the mutant and resident phenotypes go to zero [16, 17, 51]. However, because models with density-dependent dynamical variables may depend non-trivially on the phenotype under selection, a further analysis must be performed that takes into account small but non-zero phenotypic deviations. Conveniently, singular perturbation analysis not only takes nonzero phenotypic deviations into account, as a side-product it also facilitates finding sufficient conditions under which long-term evolutionary dynamics can be outlined as successive invasion implies substitution events (Figure 1).

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 clonally reproducing 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 [58, 4], 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, $\mathcal{D} := \{1, 2, \ldots, c\}$ the set of (demographic) classes where c 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 [44, 9].

Moreover, suppose that the population, at least initially, is polymorphic with respect to the trait under focus with all in all k arbitrarily distinct phenotypes, all of which define the resident population. However, as we will assume that one of the k phenotypes undergoes a mutation giving rise to a new phenotype $z_M \in \mathcal{Z}$ (M stands for mutant), thus having in total $k+1$ phenotypes in the population, we will single out its ancestral phenotype and call it the ancestral resident phenotype $z_R \in \mathcal{Z}$, or simply, the resident. The population thus consists of a mutant and a resident phenotype $z_M, z_R \in \mathcal{Z}$, respectively, as well as $k-1$ other 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 $z_{M,a}$. We emphasise that $z_{R,a}$ and $z_{M,a}$ take phenotypic value $z_R, z_M \in \mathcal{Z}$, 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 $\mathbf{n} = (n_a)_{a \in \mathcal{D}} \in \mathbb{R}_+^c$ denote the vector of densities (number of individuals per unit space) of resident individuals in all the possible classes the individuals in the population can be in, where each element $n_a \in \mathbb{R}_+$ is the density of individuals in class $a \in \mathcal{D}$. Similarly, $\mathbf{z} = (z_a)_{a \in \mathcal{D}} \in \mathcal{Z}^c$ is a resident phenotype vector where each element z_a identifies individuals in class $a \in \mathcal{D}$ with a phenotype $z \in \mathcal{Z}$. The densities of the rest of the ecological community is represented with a density vector $\mathbf{n}_P \in \mathbb{R}_+^m$, for some $m \in \mathbb{N}_+$ that depends on the size of the community. Note that the mutant phenotype is not present in the resident population, and for convenience we have included the other $k-1$ phenotypes of the population in the density vector $\mathbf{n}_P$.

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

$$\dot{\mathbf{n}} = \mathbf{H}(z, \mathbf{z}, \mathbf{n}, \mathbf{n}_P)\mathbf{n}$$
$$\dot{\mathbf{n}}_P = \mathbf{P}(\mathbf{z}, \mathbf{n}, \mathbf{n}_P),$$

$$(3)$$

where the dot " $\cdot$ " above the density vectors $\mathbf{n}$ and $\mathbf{n}_P$ denotes the time derivative " $\frac{d}{dt}$ ". The matrix $\mathbf{H} = \left(h_{ab}\right)_{a,b \in \mathcal{D}} \in \mathbb{R}^{c \times c}$ is the resident growth-rate matrix where entry $h_{ab}(z, \mathbf{z}, \mathbf{n}, \mathbf{n}_P)$ 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 $\mathbf{P} \in \mathbb{R}^{m \times m}$ is the growth-rate matrix of the rest of 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 [61], 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 $(\hat{\mathbf{n}}, \hat{\mathbf{n}}_\mathrm{P}) \in \mathbb{R}_+^{c+m}$ 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 bounded away from zero [62]. 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* [22] 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).

2.2 Mutant-resident dynamics

We now introduce the mutant phenotype $z_\mathrm{M} \in \mathcal{Z}$ into the resident population. Let $\mathbf{n}_\mathrm{R} = (n_{\mathrm{R},a})_{a \in \mathcal{D}} \in \mathbb{R}_+^c$ and $\mathbf{n}_\mathrm{M} = (n_{\mathrm{M},a})_{a \in \mathcal{D}} \in \mathbb{R}_+^c$ denote the vectors of densities and $\mathbf{z}_\mathrm{R} = (z_{\mathrm{R},a})_{a \in \mathcal{D}} \in \mathcal{Z}^c$ and $\mathbf{z}_\mathrm{M} = (z_{\mathrm{M},a})_{a \in \mathcal{D}} \in \mathcal{Z}^c$ the vectors of phenotypes of 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 $\mathbf{G} = \left(g_{a\delta}\right)_{a,\delta\in\mathcal{D}} \in \mathbb{R}^{c\times c}$ 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 $g_{a\delta}(x)$ 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 $\delta \in \mathcal{D}$ 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 resident dynamics (3), $\mathbf{R} \in \mathbb{R}^{m\times m}$ is the growth-rate matrix 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 residents $z_{\mathrm{R}} \in \mathcal{Z}$, it will be convenient to change the dynamical variables by considering the frequency of mutants $p_{\mathrm{M},a} = \frac{n_{\mathrm{M},a}}{n_{\mathrm{M},a}+n_{\mathrm{R},a}}$ 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 $\mathbf{p} = (p_{\mathrm{M},a})_{a\in\mathcal{D}} \in [0,1]^c$ and $\mathbf{n} = (n_a)_{a\in\mathcal{D}} \in \mathbb{R}_+^c$ are thus the vectors for class-specific mutant frequencies and class-specific total densities of (mutant and 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

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

where $\bar{\mathbf{G}} = (\bar{g}_{a\delta})_{a,\delta\in\mathcal{D}}$, with $\bar{g}_{a\delta} = g_{a\delta}(z_{\mathrm{M}})p_{\mathrm{M},\delta} + g_{a\delta}(z_{\mathrm{R}})p_{\mathrm{R},\delta}$, is the average mutant-resident growth-rate matrix, and where $\mathbf{F} = (f_{a\delta})_{a,\delta\in\mathcal{D}} \in \mathbb{R}^{c\times c}$ 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

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

where we have used equations (4) and (5) and the definition of class mutant frequencies $p_{\mathrm{M},a}$. Following [39], it will be useful to rewrite the above equation (6) by subtracting and adding a term $\sum_{\delta}\frac{n_\delta}{n_a}\bar{g}_{a\delta}p_{\mathrm{M},\delta}$

to obtain

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

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

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

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

$$f^{\mathrm{sel}}_{a\ell}(z_{\mathrm{M}}) = \frac{n_{\ell}}{n_a} \left[g_{a\ell}(z_{\mathrm{M}}) - \bar{g}_{a\ell} \right] \tag{8b}$$

and

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

Notice that $f^{\mathrm{sel}}_{a\ell}(z_{\mathrm{M}})$ is proportional to the difference between mutant and average growth-rates and thus captures the effect of selection (hence the superscript "sel"). The second term $f^{\mathrm{pc}}_{a\ell}$ is proportional only to the average growth-rate and because it does not involve any differences in growth-rates it captures non-selective transitions between classes. Since the relative growth-rate due to the term $f^{\mathrm{pc}}_{a\ell}$ is non-selective and thus independent of ones phenotype (Appendix 6.1), the argument present e.g. in $f^{\mathrm{sel}}_{a\ell}(z_{\mathrm{M}})$ is not included in $f^{\mathrm{pc}}_{a\ell}$, but it should nevertheless be kept in mind that $\mathbf{F}^{\mathrm{pc}}$ depends both on mutant and resident traits. Such non-selective transitions rates 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 [1, 34]), since they result from alleles changing contexts (e.g., from good habitat to bad habitat, from young to old individual). We discuss these allele frequency changes resulting from allele transmission between contexts in more detail in the next Section 2.3 and they have also been called "passive changes" (e.g. [25, 39, 41]) when the different contexts an allele can reside in are demographic classes, which is the case of the present paper (more generally changes due to transmission include recombination, mutation; see [34] for more details on the concept of the context of an allele and a discussion of transmission as an evolutionary force).

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 [22, 6, 7] and the proposition given below is an analogue to a property derived for unstructured populations in [42, 6].

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 $x \in \mathcal{Z}$. 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 $z \in \mathcal{Z}$, 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 [6] (see also [42]).

Properties of relative growth-rates Here we apply the above properties (9)-(11) to the mutant relative growth rate matrix (8). The Consistency relation (9) immediately implies that the selection component of the relative growth-rate matrix $\mathbf{F}^{\mathrm{sel}} = \mathbf{0}$ is a null matrix and hence

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

where

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

for all $a, \ell \in \mathcal{D}$. We thus confirm that under phenotypic equality selection (i.e. 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 $\mathbf{F}^{\mathrm{pc}}$. That is, under phenotypic equality it is the "passive changes" that determines the dynamics of class-specific mutant frequencies [58, 57, 4, 25, 39, 41].

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

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

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

for all $a, \ell, c \in \mathcal{D}$. 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 $\frac{\partial}{\partial z}h_{a\ell}(z)$ if one is a mutant and $\frac{\partial}{\partial z}h_{a\ell}(z)p_{\mathrm{M},\ell}$ if one is an average (random) individual in class $\ell \in \mathcal{D}$. 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 presented in this paper. If so, the fast dynamical variables would then have enough time to reach their steady state 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

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

where $\mathbf{F}_0^{\mathrm{pc}} := \mathbf{F}^{\mathrm{pc}}|_{\delta=0}$ is as given in (12). We immediately notice that as all variables $\mathbf{p}, \mathbf{n}$ and $\mathbf{n}_{\mathrm{P}}$ fluctuate at a rate dominated by the terms of order $O(1)$ 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 $p_{\mathrm{M},a}$ and thus also the mean mutant frequency $p_{\mathrm{M}} = \sum_a \frac{n_a}{n} p_{\mathrm{M},a}$ in the population (Appendix 6.3). 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 $p_{\mathrm{M},a}, \forall a \in \mathcal{D}$, thus tracking also the mean mutant frequency in the population p_{M}, we take an average of $p_{\mathrm{M},a}$ over all $a \in \mathcal{D}$ with weights chosen such that the change of this weighted average mutant frequency vanishes under phenotypic equality. In the next paragraph we show that the appropriate weights are given by the vector $\boldsymbol{\alpha} = (\alpha_a)_{a\in\mathcal{D}} \in \mathbb{R}^c$ where α_a is the class reproductive value [58, 50, 38, 54, 51, 39]. This exposition follows closely that of [39].

For the moment, let $\boldsymbol{\alpha}$ be an arbitrary vector normalized as $\sum_a \alpha_a = 1$, 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 differentiate with respect to time t and obtain

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

where we have used (5) and (8). Now, the class reproductive values are defined such that for any frequency distributions $\mathbf{p}$ they in some sense "cancel" the class transitions due to passive changes [25, 39], rendering

the dynamics of the weighted frequency (17) solely in 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

$$\dot{\boldsymbol{\alpha}} = -\boldsymbol{\alpha}\mathbf{F}^{\mathrm{pc}}, \qquad \boldsymbol{\alpha}(t=0) := \boldsymbol{\alpha}_0, \tag{18}$$

where $\mathbf{F}^{\mathrm{pc}}$ is as in (8) (see Appendix 6.2). Note that as $\sum_b f_{ab} = 0$ the matrix $\mathbf{F}^{\mathrm{pc}}$ is the infinitesimal generator matrix for a continuous-time mutant-resident markov chain $\boldsymbol{\alpha}$ on the state space $\mathcal{D}$. Using the ODE (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 the ODE in (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). Remarkably, 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). The general interpretation of the class-specific reproductive value α_a is hence the probability that given a random individual is taken from a random class at any point in time t, its lineage (e.g. its parent due to a birth event) came from class $a \in \mathcal{D}$ one unit of time ago [51, 40]. This interpretation holds both in fast and slow time.

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 $\hat{\mathbf{F}}_0^{\mathrm{pc}} = \mathbf{F}_0^{\mathrm{pc}}(\mathbf{z}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_{\mathrm{P}})$. 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. Therefore, $\hat{\alpha}_a$ can be interpreted as the asymptotic probability that the ancestral lineage of a random individual was in class $a \in \mathcal{D}$. That is, $\hat{\boldsymbol{\alpha}}$ can be defined as the long-term contribution of individuals, in a given class, to the future [51, 41] (see further discussion in Appendix 6.2). We note that because the mutant frequency fluctuates (also) in slow evolutionary time (20), the long-term interpretation of $\hat{\boldsymbol{\alpha}}$ holds only under phenotypic equality as only then the matrix $\hat{\mathbf{F}}_0^{\mathrm{pc}}$ is frequency independent.

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) (20) the dynamics of p_α 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 $O(1)$. It will thus become sufficient to study the dynamics of $\boldsymbol{\alpha}, \mathbf{p}, \mathbf{n}$ and $\mathbf{n}_\mathrm{P}$ under phenotypic equality ($\delta = 0$), which is given by

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

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

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

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 calculate from (21). The remaining task is to find the steady state $\hat{\mathbf{p}}$, which can be solved from

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

$$
\Longleftrightarrow
$$

$$
\sum_{b} f_{ab}^{\mathrm{pc}}(\mathbf{z}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_\mathrm{P})\Big|_{\delta=0} \hat{p}_{\mathrm{M},b} = \sum_{b} \frac{n_b}{n_a} h_{ab}(z, \mathbf{z}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_\mathrm{P})(\hat{p}_{\mathrm{M},b} - \hat{p}_{\mathrm{M},a}) = 0 \qquad \forall a \in \mathcal{D},
\tag{24}
$$

16

and is given by

$$\hat{\mathbf{p}} = (\hat{p}_{M,1}, \ldots, \hat{p}_{M,c}) = (p, \ldots, p), \tag{25}$$

where the class-specific mutant frequencies $p_{M,a}$ in all classes $a \in \mathcal{D}$ are equal. The exact value of $p \in [0,1]$ to which the class mutant frequencies $p_{M,a}$ approach to, $\forall a \in \mathcal{D}$, 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, and under phenotypic equality the weighted average frequency is constant $\dot{p}_\alpha = 0$ as shown in Section 3.1, we must have that $\boldsymbol{\alpha}(0)\mathbf{p}(0) = p_\alpha(0) = \lim_{t\to\infty} p_\alpha(t) = \sum_a \hat{\alpha}_a \hat{p}_{M,a}$, and so $\hat{p}_{M,a} = p_\alpha$ for all $a \in \mathcal{D}$, since the equilibrium frequencies are the same in each class.

We have thus obtained that whenever the mutant and resident phenotypes are equal $\delta = 0$, the dynamics given by (22) approaches in fast population dynamical time the steady state $(\hat{\boldsymbol{\alpha}}, \hat{\mathbf{p}}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_P)$, which we will represent as the critical manifold:

$$\mathcal{M}_0 = \{(\hat{\boldsymbol{\alpha}}, \hat{\mathbf{p}}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_P) \in \mathbb{R}^{c+c+c+m} \mid \hat{p}_{M,a} = p_\alpha \; \forall a \in \mathcal{D}\}, \tag{26}$$

where the subscript 0 indicates that we are studying the case where $\delta = 0$ (see Figure 3). Because $(\hat{\mathbf{n}}, \hat{\mathbf{n}}_P)$ is hyperbolic and the critical equilibrium manifold $\mathcal{M}_0$ is compact (the set of points are bounded and closed) consisting of a neutral line of equilibria (due to the term $\hat{\mathbf{p}}$), it follows that $\mathcal{M}_0$ is compact and a normally hyperbolic invariant manifold [62]. 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 trivially invariant).

Perturbed manifold As elucidated above, the critical manifold $\mathcal{M}_0$ is compact and normally hyperbolic, and therefore the results in [18, 19, 20, 21, 32] (see e.g. Theorem 9.1. in [21] or in a more recent account Theorem 2 page 354 in [31]) guarantee that a perturbed (invariant) manifold $\mathcal{M}_\delta$ for the mutant-resident dynamics under phenotypic similarity (δ small) exists, is close to, and has identical stability properties as $\mathcal{M}_0$ (see also Figure 3). A perturbed manifold is thus a set of points that are invariant under the flow of the (perturbed) mutant-resident dynamics for small but nonzero δ (unlike $\mathcal{M}_0$ it doesn't consist of an infinite number of equilibria) while in the neighborhood of $\mathcal{M}_\delta$ and $\mathcal{M}_0$ the dynamics is equivalent. Moreover, the dynamics of a slow dynamical variable p_α when restricted to $\mathcal{M}_0$ (in slow time) and $\mathcal{M}_\delta$ are also equivalent. 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.

4   Invasion implies substitution

We now the 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
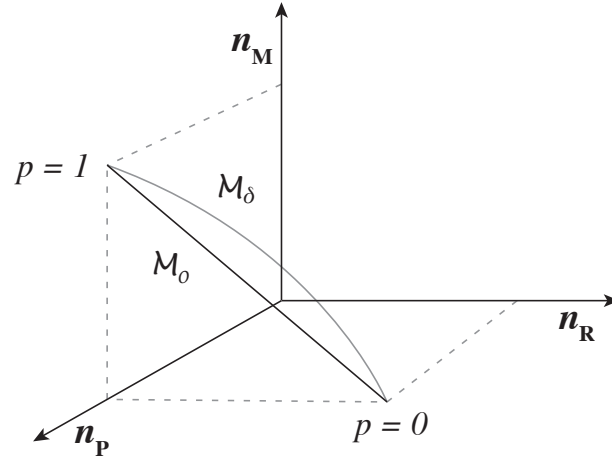
Figure 3: Critical and perturbed manifolds $\mathcal{M}_0$ and $\mathcal{M}_\delta$, respectively. The critical manifold $\mathcal{M}_0$ consists of a line (infinite number) of equilibria and is obtained by solving the equation (23). Because $\mathcal{M}_0$ is a normally hyperbolic invariant manifold, there exists a perturbed manifold $\mathcal{M}_\delta$ which is close to $\mathcal{M}_0$ and has the same dynamical properties as $\mathcal{M}_0$ [21, 31, 35]. Importantly, the dynamics of p_α for small δ on $\mathcal{M}_\delta$ and the dynamics of p_α for $\delta = 0$ on $\mathcal{M}_0$ are equivalent.

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 $\mathbf{p}$, resident densities $\mathbf{n}$ and the densities of the rest of the ecological community $\mathbf{n}_{\mathrm{P}}$, 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:

$$
\begin{aligned}
\dot{p}_\alpha &= \boldsymbol{\alpha}\mathbf{F}^{\mathrm{sel}}(z_{\mathrm{M}})\mathbf{p} \\
\dot{\boldsymbol{\alpha}} &= -\boldsymbol{\alpha}\mathbf{F}^{\mathrm{pc}} \\
\dot{\mathbf{p}} &= \mathbf{F}(z_{\mathrm{M}})\mathbf{p} \\
\dot{\mathbf{n}} &= \bar{\mathbf{G}}\mathbf{n} \\
\dot{\mathbf{n}}_{\mathrm{P}} &= \mathbf{R}.
\end{aligned}
\tag{27}
$$

Next, we write the dynamics of (27) 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 [21, 33, 31, 35]. By doing this the singular system ($\delta = 0$) serves as an approximation to a mutant-resident dynamics under phenotypic similarity (δ small) 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) either using the

original time variable t

$$
\begin{aligned}
\frac{\mathrm{d}p_\alpha(t)}{\mathrm{d}t} &= \delta\boldsymbol{\alpha}\frac{\mathrm{d}}{\mathrm{d}\delta}\mathbf{F}^{\mathrm{sel}}(z_{\mathrm{M}})\Big|_{\delta=0}\mathbf{p} + O(\delta^2) \\
\frac{\mathrm{d}\boldsymbol{\alpha}(t)}{\mathrm{d}t} &= -\boldsymbol{\alpha}(t)\mathbf{F}^{\mathrm{pc}}_0 + O(\delta) \\
\frac{\mathrm{d}\mathbf{p}(t)}{\mathrm{d}t} &= \mathbf{F}^{\mathrm{pc}}_0\mathbf{p}(t) + O(\delta) \\
\frac{\mathrm{d}\mathbf{n}(t)}{\mathrm{d}t} &= \mathbf{H}(z)\mathbf{n}(t) + O(\delta) \\
\frac{\mathrm{d}\mathbf{n}_{\mathrm{P}}(t)}{\mathrm{d}t} &= \mathbf{P} + O(\delta)
\end{aligned}
\tag{28}
$$

or using the new time variable τ

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

Since we haven't yet taken any limits the two systems (28) and (29) 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

$$
\begin{aligned}
\frac{dp_\alpha(t)}{dt} &= 0 \\
\frac{d\boldsymbol{\alpha}(t)}{dt} &= -\boldsymbol{\alpha}(t)\mathbf{F}^{\mathrm{pc}}_0 \\
\frac{d\mathbf{p}(t)}{dt} &= \mathbf{F}^{\mathrm{pc}}_0\mathbf{p}(t) \\
\frac{d\mathbf{n}(t)}{dt} &= \mathbf{H}(z)\mathbf{n}(t) \\
\frac{d\mathbf{n}_{\mathrm{P}}(t)}{dt} &= \mathbf{P}
\end{aligned}
\tag{30}
$$

and the second for slow evolutionary time

$$
\begin{aligned}
\frac{dp_\alpha(\tau)}{d\tau} &= \boldsymbol{\alpha}\frac{d}{d\delta}\mathbf{F}^{\mathrm{sel}}(z_{\mathrm{M}})\Big|_{\delta=0}\mathbf{p} \\
0 &= -\boldsymbol{\alpha}(\tau)\mathbf{F}^{\mathrm{pc}}_0 \\
0 &= \mathbf{F}_0\mathbf{p}(\tau) \\
0 &= \mathbf{H}(z)\mathbf{n}(\tau) \\
0 &= \mathbf{P}.
\end{aligned}
\tag{31}
$$

This confirms that in the fast population dynamical time (30) the average mutant frequency p_α stays constant and that the mutant-resident dynamics reaches the critical manifold $\mathcal{M}_0$ as found in (26), and

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that the algebraic expression for $\mathcal{M}_0$ can be obtained directly from (31).

Because the variables $\boldsymbol{\alpha}, \mathbf{p}, \mathbf{n}, \mathbf{n}_P$ in (31) have reached their critical manifold $\mathcal{M}_0$, we evaluate the right hand side of the first line in (31) at the $\mathcal{M}_0$ to obtain

$$
\left[\hat{\boldsymbol{\alpha}} \frac{d}{d\delta} \mathbf{F}^{\text{sel}} \Big|_{\delta=0} \hat{\mathbf{p}} \right]_{\mathcal{M}_0} = \sum_a \hat{\alpha}_a \sum_b \left(\frac{\partial}{\partial z_{\text{M}}} f_{ab}^{\text{sel}}(z_{\text{M}}) + \sum_c \frac{\partial}{\partial z_{\text{M},c}} f_{ab}^{\text{sel}}(z_{\text{M}}) \right)_{\substack{\delta=0 \\ \mathcal{M}_0}} \hat{p}_{\text{M},b}
$$
$$
= \sum_a \hat{\alpha}_a \sum_b \frac{\hat{n}_b}{\hat{n}_a} \frac{\partial}{\partial z} h_{ab}(z, \mathbf{z}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_P) p(1-p)
$$
(32)

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 6.2 for more details), then at $\mathcal{M}_0$ we have

$$
\hat{v}_a = \frac{\hat{\alpha}_a}{\hat{n}_a},
$$
(33)

and using (32) we can write the slow (singular) mutant-resident evolutionary dynamics (31) constrained on $\mathcal{M}_0$ with a single equation as

$$
\frac{dp_\alpha(\tau)}{d\tau} \Big|_{\mathcal{M}_0} = p_\alpha(1 - p_\alpha) \sum_{a,b} \hat{v}_a \frac{\partial h_{ab}(z)}{\partial z} \hat{n}_b
$$
(34)

or in a matrix notation as

$$
\frac{dp_\alpha(\tau)}{d\tau} \Big|_{\mathcal{M}_0} = p_\alpha(1 - p_\alpha) \hat{\mathbf{v}} \frac{\partial \mathbf{H}(z)}{\partial z} \hat{\mathbf{n}}.
$$
(35)

Now, geometric singular perturbation theory guarantees that the mutant-resident dynamics (28)-(29), and in particular the dynamics of the weighted mutant frequency p_α constrained on $\mathcal{M}_\delta$, is equivalent to the singular evolutionary dynamics of p_α constrained on $\mathcal{M}_0$ as in (35). We have thus proved the below "invasion implies substitution" Theorem 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 $(\hat{\mathbf{n}}, \hat{\mathbf{n}}_P) \in \mathbb{R}^{N+m}$ to which the resident population converges to and then stays at.*

Theorem (invasion implies substitution). *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 small δ, the mutant-resident ecological community (4) converges in fast population dynamical time to a manifold $\mathcal{M}_\delta$ which is a small perturbation away from the critical equilibrium manifold*

$$
\mathcal{M}_0 = \{ (\hat{\boldsymbol{\alpha}}, \hat{\mathbf{p}}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_P) \in \mathbb{R}^{c+c+c+m} \mid \hat{p}_{M,a} = p_\alpha \; \forall a \in \mathcal{D} \},
$$
(36)

after which the dynamics of the weighted mutant frequency p_α on $\mathcal{M}_\delta$ can be approximated by the dynamics of p_α on $\mathcal{M}_0$ which is given by

$$\left.\frac{dp_\alpha(\tau)}{d\tau}\right|_{\mathcal{M}_0} = p_\alpha(1 - p_\alpha)\hat{\boldsymbol{v}}\frac{\partial \mathbf{H}(z)}{\partial z}\hat{\mathbf{n}}. \tag{37}$$

Because $p_M|_{\mathcal{M}_0}$ is proportional to p_α, the mean mutant frequency p_M either monotonically decreases or increases for all $p_M \in (0,1)$ depending on the sign of the frequency-independent selection gradient

$$S(z) = \hat{\boldsymbol{v}}\frac{\partial \mathbf{H}(z, \mathbf{z}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_P)}{\partial z}\hat{\mathbf{n}}. \tag{38}$$

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

Corollary (C). *The subset of $\mathcal{Z}$ where the assumption (A) holds and where the selection gradient (38) is nonzero determines the set of phenotypic values where successive invasion implies substitution events may occur, i.e. it defines a set of trait-substitutions.*

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 [21, 31, 7] the mutant-resident dynamics using the phenotypic deviation δ as the perturbation parameter. In this method 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 $\dot{x} = u(x, p, \delta)$, $\dot{p} = \delta v(x, p, \delta)$ 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 [58, 38, 51, 37, 13, 36, 40, 39].

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 formidable 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 $\dot{x} = u(x, p, 0)$, and the other in slow time where x is constant (i.e. is at the steady state) and p fluctuates according to $\frac{d}{d\tau} = v(x, p, 0)$. 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 the final step one perturbs the above singular equations by applying geometric singular perturbation results developed in [21]. Provided certain conditions are satisfied, one can then equate the dynamics of the singular equations with the original system we started from where δ was 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 mutant-resident dynamics whenever the steady state is hyperbolic.

Interestingly, 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 [21] allow a direct generalization of our result to models with attractors other than equilibria as considered here, 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 [39]) we choose to leave this generalization for future work. Second, more recent but equivalent results on invariant manifolds for semiflows [3, 2, 35] accommodate a more general demographic (physiological) structure, in particular, allowing continuous structuring variables e.g. continuous age or size distributions. However, calculating the hyperbolicity of steady states is considerably more involved in such cases [26, 27, 35].

Selection gradient as a map between ecology and evolution   The expression for the selection gradient (38) 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), with the exception that in our model the relatedness matrix $\mathbf{R}$ plays no role. This is because we assume infinitely large population sizes with no spatial structure 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 (density dependence) has been previously considered in [40, 39]. However, the model and the method obtaining the selection gradient depart from ours in that in [40, 39] the polymorphism is assumed tightly clustered around its mean and that the dynamical equations were formulated in terms of a Price equation.

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 treatment in [40, 39] is also the first (but see [37]) in utilizing class-reproductive values defined for arbitrary phenotypic deviations and as functions of fast population dynamical variables – both properties that need to be taken into account in the full proof of the "invasion implies substitution"-principle. 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 the class-specific trait variance is indeed a fast variable approaching the population mean trait variance, a result that was left open in [41]. We conjecture that the ideas on tightly clustered phenotypes developed in [42] together with the results derived in this paper fully justify the selection gradient presented in [40, 39].

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 [24, 49, 7]. 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). Here we proceed the same way with the exception that we don't specify the phenotype of the individual whose relative growth-rate we are calculating

$$
\begin{aligned}
\dot{p}_{\mathrm{X},a} &= \frac{d}{dt}\left(\frac{n_{\mathrm{X},a}}{n_a}\right) = \frac{\dot{n}_{\mathrm{X},a}n_a - n_{\mathrm{X},a}\dot{n}_a}{n_a^2} \\
&= \frac{1}{n_a}\left[\dot{n}_{\mathrm{X},a} - p_{\mathrm{X},a}\dot{n}_a\right] \\
&= \sum_{\mathit{b}}\frac{n_{\mathit{b}}}{n_a}g_{a\mathit{b}}(z_{\mathrm{X}})p_{\mathrm{X},\mathit{b}} - p_{\mathrm{X},a}\sum_{\mathit{b}}\frac{n_{\mathit{b}}}{n_a}\left(g_{a\mathit{b}}(z_{\mathrm{M}})p_{\mathrm{M},a} + g_{a\mathit{b}}(z_{\mathrm{R}})p_{\mathrm{R},a}\right) \\
&= \sum_{\mathit{b}}\frac{n_{\mathit{b}}}{n_a}g_{a\mathit{b}}(z_{\mathrm{X}})p_{\mathrm{X},\mathit{b}} - p_{\mathrm{X},a}\sum_{\mathit{b}}\frac{n_{\mathit{b}}}{n_a}\bar{g}_{a\mathit{b}} \\
&= \sum_{\mathit{b}}\frac{n_{\mathit{b}}}{n_a}g_{a\mathit{b}}(z_{\mathrm{X}})p_{\mathrm{X},\mathit{b}} - p_{\mathrm{X},\mathit{b}}\sum_{\mathit{b}}\frac{n_{\mathit{b}}}{n_a}\bar{g}_{a\mathit{b}} + p_{\mathrm{X},\mathit{b}}\sum_{\mathit{b}}\frac{n_{\mathit{b}}}{n_a}\bar{g}_{a\mathit{b}} - p_{\mathrm{X},a}\sum_{\mathit{b}}\frac{n_{\mathit{b}}}{n_a}\bar{g}_{a\mathit{b}} \\
&= \sum_{\mathit{b}}\frac{n_{\mathit{b}}}{n_a}\left[g_{a\mathit{b}}(z_{\mathrm{X}}) - \bar{g}_{a\mathit{b}}\right]p_{\mathrm{X},\mathit{b}} + p_{\mathrm{X},\mathit{b}}\sum_{\mathit{b}\neq a}\frac{n_{\mathit{b}}}{n_a}\bar{g}_{a\mathit{b}} - p_{\mathrm{X},a}\sum_{\mathit{b}\neq a}\frac{n_{\mathit{b}}}{n_a}\bar{g}_{a\mathit{b}}
\end{aligned}
\tag{39}
$$

for all $a \in \mathcal{D}$, where $\bar{g}_{a\mathit{b}} = g_{a\mathit{b}}(z_{\mathrm{M}})p_{\mathrm{M},\mathit{b}} + g_{a\mathit{b}}(z_{\mathrm{R}})p_{\mathrm{R},\mathit{b}}$ and where $z_{\mathrm{X}} \in \{z_{\mathrm{M}}, z_{\mathrm{R}}\}$. 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

$$
\begin{aligned}
\dot{\mathbf{p}}_{\mathrm{X}} &= \mathbf{F}(z_{\mathrm{X}})\mathbf{p}_{\mathrm{X}} \\
&= \left[\mathbf{F}^{\mathrm{pc}}(z_{\mathrm{X}}) + \mathbf{F}^{\mathrm{pc}}\right]\mathbf{p}_{\mathrm{X}}
\end{aligned}
\tag{40}
$$

where $z_{\mathrm{X}} \in \{z_{\mathrm{M}}, z_{\mathrm{R}}\}$ and $\mathbf{p}_{\mathrm{X}} \in \{\mathbf{p}_{\mathrm{M}}, \mathbf{p}_{\mathrm{R}}\}$ and where the entries of $\mathbf{F}^{\mathrm{pc}}(z_{\mathrm{X}})$ and $\mathbf{F}^{\mathrm{pc}}(z_{\mathrm{X}})$, respectively, are

$$
f_{a\mathit{b}}^{\mathrm{sel}}(z_{\mathrm{X}}) = \frac{n_{\mathit{b}}}{n_a}\left[g_{a\mathit{b}}(z_{\mathrm{X}}) - \bar{g}_{a\mathit{b}}\right]
$$

$$
f_{a\mathit{b}}^{\mathrm{pc}} = \begin{cases} \frac{n_{\mathit{b}}}{n_a}\bar{g}_{a\mathit{b}} & \forall \mathit{b} \neq a \\ -\sum_{c \neq a}\frac{n_c}{n_a}\bar{g}_{ac}, & \text{for } \mathit{b} = a. \end{cases}
\tag{41}
$$

Notice that the component that gives the rates at which passive changes occur $\mathbf{F}^{\mathrm{pc}}$ 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 Individual reproductive values

This exposition follows closely that of [39] with the exception on how we define the individual-specific reproductive values. The main insight is that in contrast to standard practice the reproductive values are not calculated at the steady state and are thus defined in both fast population dynamical as well as slow evolutionary time (see a more detailed discussion in [39]).

In the main text we discussed the general definition for class reproductive values, and here we complement this analysis by giving a general definition for individual reproductive values. In contrast to [58, 40, 39] where the individual reproductive value is defined as $\frac{\alpha_a}{\pi_a}$, we define an individual reproductive value as

$$v_a = \frac{\alpha_a}{n_a}, \qquad \forall a \in \mathcal{D}. \tag{42}$$

Because v_a is a function of time and we are interested in its dynamics, lets differentiate and obtain

$$
\begin{aligned}
\dot{v}_a &= \frac{1}{n_a}\dot{\alpha}_a - \frac{1}{n_a}v_a\dot{n}_a \\
&= -\frac{1}{n_a}\left[\sum_{b}\alpha_b\frac{n_a}{n_b}\bar{g}_{ba} - \alpha_a\sum_{b}\frac{n_b}{n_a}\bar{g}_{ab}\right] - \frac{1}{n_a}v_a\sum_{b}\bar{g}_{ab}n_b \\
&= -\sum_{b}v_b\bar{g}_{ba} + v_a\sum_{b}\frac{n_b}{n_a}\bar{g}_{ab} - v_a\sum_{b}\frac{n_b}{n_a}\bar{g}_{ab} \\
&= -\sum_{b}v_b\bar{g}_{ba}, , \qquad \forall a \in \mathcal{D},
\end{aligned}
\tag{43}
$$

which can be expressed with a matrix notation as

$$\dot{\mathbf{v}} = -\mathbf{v}\bar{\mathbf{G}}, \tag{44}$$

where $\mathbf{v} = (v_a)_{a\in\mathcal{D}}$ is a vector of individual reproductive values. Similarly to class reproductive values, individual reproductive values as defined in (44) are both fast and slow variables. Using (44) and Section 2.3 the slow evolutionary time definition under phenotypic equality $\delta = 0$ is

$$\mathbf{0} = \hat{\mathbf{v}}\mathbf{H}(z, \mathbf{z}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_{\mathrm{P}}), \tag{45}$$

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.

6.3 Mean mutant frequency p_{M} as a fast population dynamical and slow evolutionary variable

In the main text we showed that class-specific mutant frequencies $\mathbf{p}$ are both fast and slow variables, i.e. under phenotypic similarity the dynamics is dominated by the terms of order $O(1)$ and it approaches a line of equilibria at which the dynamics is dominated by the terms of order $O(\delta)$. Here we confirm that the same applies for the mean mutant frequency in the total population $p_{\mathrm{M}} = \boldsymbol{\pi}\mathbf{p} = \sum_a \pi_a p_{\mathrm{M},a}$. We do this by showing that class frequencies $\boldsymbol{\pi}$ under phenotypic similarity are dominated by the terms of order $O(1)$ and approach an (isolated) equilibrium value (i.e. $\boldsymbol{\pi}$ doesn't change in slow time). For completeness, we study both the resident and mutant-resident dynamics of class frequencies.

Resident Dynamics Define $\pi_a = \frac{n_a}{n}$, where $n = \sum_a n_a$, as the proportion of resident individuals inhabiting class $a \in \mathcal{D}$ in the resident ecological community (Section 2.1), that is, the probability that a randomly sampled resident individual is in class $a \in \mathcal{D}$. We obtain a dynamical equation for $\boldsymbol{\pi} = (\pi_a)_{a\in\mathcal{D}}$

by differentiation

$$
\begin{aligned}
\dot{\pi}_a &= \frac{\dot{n}_a}{n} - \frac{n_a}{n^2}\dot{n} \\
&= \frac{1}{n}\sum_{\ell} h_{a,\ell}(z)n_{\ell} - \pi_a \frac{1}{n}\sum_c\sum_{\ell} h_{c,\ell}(z)n_{\ell} \\
&= \sum_{\ell} h_{a,\ell}(z)\pi_{\ell} - \pi_a \sum_c\sum_{\ell} h_{c,\ell}(z)\pi_{\ell} \\
&= \sum_{\ell}\left[h_{a,\ell}(z) - \pi_a\sum_c h_{c,\ell}(z) \right]\pi_{\ell}, \quad \forall a \in \mathcal{D},
\end{aligned}
\tag{46}
$$

or in short,

$$
\dot{\boldsymbol{\pi}} = \mathbf{Q}(z, \mathbf{z}, \boldsymbol{\pi}, n, \mathbf{n}_{\mathrm{P}})\boldsymbol{\pi},
\tag{47}
$$

where $\mathbf{Q}(z, \mathbf{z}, \boldsymbol{\pi}, n, \mathbf{n}_{\mathrm{P}}) := \mathbf{Q}(z)$, $\mathbf{Q}(z) = (q_{a,\ell}(z))_{a,\ell\in\mathcal{D}}$ and

$$
q_{a,\ell}(z) = h_{a,\ell}(z) - \pi_a\sum_c h_{c,\ell}(z).
\tag{48}
$$

We can immediately confirm that $\sum_a q_{a,\ell}(z) = 0$ and hence $\mathbf{Q}$ is the infinitesimal generator matrix for a continuous-time markov chain on the state space $\mathcal{D}$, where $\boldsymbol{\pi}$ is the vector giving the probabilities for a resident individual being in a particular class.

Mutant-Resident Dynamics Similarly to the resident dynamics above, define $\pi_{\mathrm{M},a} = \frac{n_{\mathrm{M},a}}{n_{\mathrm{M}}}$, where $n_{\mathrm{M}} = \sum_a n_{\mathrm{M},a}$, as the frequency of mutant individuals in class $a \in \mathcal{D}$ amongst all mutants in the mutant-resident ecological community (Section 2.2), that is, the probability that given a mutant individual is sampled from the population it is in class $a \in \mathcal{D}$. We obtain a dynamical equation for $\boldsymbol{\pi}_{\mathrm{M}} = (\pi_{\mathrm{M},a})_{a\in\mathcal{D}}$ by differentiation

$$
\begin{aligned}
\dot{\pi}_{\mathrm{M},a} &= \frac{\dot{n}_{\mathrm{M},a}}{n_{\mathrm{M}}} - \frac{n_{\mathrm{M},a}}{n_{\mathrm{M}}^2}\dot{n}_{\mathrm{M}} \\
&= \frac{1}{n_{\mathrm{M}}}\sum_{\ell} g^{\mathrm{M}}_{a,\ell}(z_{\mathrm{M}})n_{\mathrm{M},\ell} - \pi_{\mathrm{M},a}\frac{1}{n_{\mathrm{M}}}\sum_c\sum_{\ell} g^{\mathrm{M}}_{c,\ell}(z_{\mathrm{M}})n_{\mathrm{M},\ell} \\
&= \sum_{\ell} g^{\mathrm{M}}_{a,\ell}(z_{\mathrm{M}})\pi_{\mathrm{M},\ell} - \pi_{\mathrm{M},a}\sum_c\sum_{\ell} g^{\mathrm{M}}_{c,\ell}(z_{\mathrm{M}})\pi_{\mathrm{M},\ell} \\
&= \sum_{\ell}\left[g^{\mathrm{M}}_{a,\ell}(z_{\mathrm{M}}) - \pi_{\mathrm{M},a}\sum_c g^{\mathrm{M}}_{c,\ell}(z_{\mathrm{M}}) \right]\pi_{\mathrm{M},\ell}, \quad \forall a \in \mathcal{D},
\end{aligned}
\tag{49}
$$

or in short,

$$
\dot{\boldsymbol{\pi}}_{\mathrm{M}} = \mathbf{T}(z_{\mathrm{M}}, \mathbf{z}_{\mathrm{R}}, \mathbf{z}_{\mathrm{M}}, \boldsymbol{\pi}_{\mathrm{M}}, n_{\mathrm{M}}, \mathbf{n}_{\mathrm{P}})\boldsymbol{\pi},
\tag{50}
$$

where $\mathbf{T}(z_M, \mathbf{z}_R, \mathbf{z}_M, \boldsymbol{\pi}_M, n_M, \mathbf{n}_P) := \mathbf{T}(z)$, $\mathbf{T}(z_M) = (t_{a,b}(z))_{a,b \in \mathcal{D}}$ and

$$t_{a,b}(z) = g_{a,b}^M(z_M) - \pi_{M,a} \sum_c g_{c,b}^M(z_M). \tag{51}$$

We can immediately confirm that $\sum_a t_{a,b}(z_M) = 0$ and hence $\mathbf{T}$ is the infinitesimal generator matrix for a continuous-time mutant-resident markov chain on the state space $\mathcal{D}$, where $\boldsymbol{\pi}_M$ is the vector giving the probabilities for a mutant individual being in a particular class.

Mutant-Resident Dynamics under neutrality Using the consistency relation (9) from Section 2.3 we immediately obtain that under neutrality the system (50) reduces to

$$\dot{\boldsymbol{\pi}}_M = \mathbf{Q}(z, \mathbf{z}, \boldsymbol{\pi}_M, n, \mathbf{n}_P)\boldsymbol{\pi}_M, \tag{52}$$

where

$$q_{a,b}(z, \mathbf{z}, \boldsymbol{\pi}_M, n, \mathbf{n}_P) = h_{a,b}(z) - \pi_{M,a} \sum_c h_{c,b}(z). \tag{53}$$

Note, in particular, that under phenotypic equality the dynamics of elements $\pi_{M,a}$, $a \in \mathcal{D}$, is non-zero and thus $\pi_{M,a}$ are fast population dynamical variables.

The dynamics and stationary solutions $\hat{\boldsymbol{\pi}}$ and $\hat{\boldsymbol{\pi}}_M$ under neutrality From Section 3.2 we know that when mutant and resident phenotypes are equal (selective neutrality) the class-specific mutant frequencies and the densities of the ecological community approach a steady state $(\hat{\mathbf{p}}, \hat{\mathbf{n}}, \hat{\mathbf{n}}_P)$ where $\hat{\mathbf{p}} = (\hat{p}_{M,a})$ and $\hat{p}_{M,a} = p$ for all $a \in \mathcal{D}$. Consequently,

$$\begin{aligned}
\hat{\pi}_a &= \frac{\hat{n}_a}{\hat{n}} \\
\hat{p}_M &= \sum_a \hat{p}_{M,a} \hat{\pi}_a = p \\
\hat{\pi}_{M,a} &= \frac{\hat{n}_{M,a}}{\hat{n}_M} = \frac{\hat{p}_{M,a}}{\hat{p}_M} \frac{\hat{n}_a}{\hat{n}} = \frac{\hat{n}_a}{\hat{n}},
\end{aligned} \tag{54}$$

that is

$$\hat{\boldsymbol{\pi}}_M = \hat{\boldsymbol{\pi}} = \left(\frac{\hat{n}_a}{\hat{n}}\right)_{a \in \mathcal{D}}. \tag{55}$$

Thus, at the stationary state under phenotypic equality the probability that a randomly sampled mutant in the mutant-resident community is in class $a \in \mathcal{D}$ is identical to the probability that a randomly sampled individual in the resident community is in class $a \in \mathcal{D}$. Moreover, $\boldsymbol{\pi}_M$ and $\boldsymbol{\pi}$ approach the stationary state $\hat{\boldsymbol{\pi}}$ in fast population dynamical time.

Finally, because the steady state $\hat{\mathbf{n}}$ is hyperbolic it persist under small perturbations of δ and hence we can conclude that under phenotypic similarity the class frequencies $\boldsymbol{\pi}$ approach in fast population dynamical time an (isolated) equilibrium (i.e. $\boldsymbol{\pi}$ doesn't change in slow time). Therefore, the mean

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mutant frequency $p_{\mathrm{M}} = \boldsymbol{\pi}\mathbf{p} = \sum_{a}\pi_{a}p_{\mathrm{M},a}$ is both fast population dynamical and slow evolutionary variable. Moreover, in slow evolutionary time the class-specific mutant frequencies are all p and hence in slow evolutionary time $p_{\mathrm{M}} = p$.