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On the adaptational significance of migration under resource regeneration

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Abstract

Community adaptation to locally variable environments is modeled, where the environments provide density- and capacity-regulated resources for reproduction of self-replicating genetic types. Adaptational success or failure is assessed in terms of community persistence. A community's adaptational strategy to its environments is specified by reproductive responses of genotypes (reproduction norms) to and migration among environments. It is adaptationally successful only to the degree to which it guarantees sustainable utilization of the environmental resources. Combined analytical and numerical evaluation of the model, and its special approach to the notion of adaptation, allow several unconventional insights into the interplay between selection and migration. Analysis of scenarios of habitat choice (genetic types differ in migrational preferences for environments) and habitat fragmentation (local isolation through constrained migration) help demonstrate the relevance of the findings. Among these are: • migration can reverse selection effects, and density regulation can reverse adaptational tendencies, and this is rather the rule than the exception, • strategies for avoidance of over-exploitation rely on mutual immigration of less reproductive genotypes (establishing mutual selection-immigration balances between environments/locations), • genetic variation among environments can thus aid in reducing over-exploitation and by this support adaptation, • if selection-immigration balances fail and resource depletion proceeds, local extinction risks can be reduced by adjusting the local emigration rates that determine stationary reproduction, • the greatest challenges to adaptational strategies are posed by

weak density regulation, while strong regulation challenges adaptational perfection rather than facilitating adaptational failure, • extinction risks can be more readily compensated under local than under global density regulation. These findings help substantiate several common concepts of (evolutionary) adaptation, including evolutionary rescue and suicide as the results of success or failure in establishing sustainable resource utilization.

Keywords: adaptational strategy for community persistence, balancing genetic polymorphism, density and capacity regulation, evolutionary rescue and suicide, genotype-environment associations, habitat choice, habitat fragmentation, local and global density regulation, reproduction norm of reaction, selection-migration balance, sustainable utilization of resources

1 Introduction

The present topic is motivated by the observation that studies of evolutionary adaptation and its contributing forces (including migration) mostly seem to focus on stably sustainable community densities. Adaptational success, however, is preferably assessed in terms of communities' (per capita) multiplication rates (cf. e.g. the Special Feature published by Brady et al., 2019, and authored by a large working group on concepts of maladaptation). Rates exceeding 1 imply continuing community growth, but adherence to this is unrealistic in the face of generally limited resources for reproduction. At the other extreme, rates continuously falling below 1 imply ultimate community extinction. Hence, successful adaptation entails rates that stabilize at a value of 1.

Yet, multiplication rates of 1 can be realized at almost arbitrary levels of community density and are therefore inadequate indicators of adaptational processes that safeguard stable community persistence (Brady et al., 2019, p.506, right column). While this seems trivial, it nevertheless has the basic implication that adaptation cannot be understood without specific reference to the forces regulating community density. For successful adaptation, these forces should at least allow for the evolution of adequate densities over generations. Herewith, multiplication rates close to 1 are implied, but they are not suitable indicators of the establishment of viable community densities.

In other cases, adaptational processes are associated with the progress of genetic or species diversity in communities or metacommunities. This "classic evolutionary view" of adaptation is focused on relative genotype frequencies (Brady et al., 2019, p.496) and by this allows for no direct assessments of density dynamics. Indeed, in the review of Chesson (2000) on mechanisms of maintenance of species diversity, the term adaptation does not even appear. Brady et al. continue their review on the same page with the statement that by contrast, under the "classic ecological view ... a growing or stable population is perceived to be well adapted to present conditions, whereas a population in decline suggests maladaptation".

The considerable work on integration of the two views particularly in the field of evolutionary ecology is acknowledged by the authors but still deemed worthy of directing attention more explicitly to concepts of adaptation and maladaptation in

particular. The distinction between relative and absolute fitness is argued to be essential in this respect (for a more recent example see Yamamichi et al., 2023, which also has review character). In view of the basic observation that unconditional adaptational failure results in continual reduction of community density and thus in ultimate extinction, this distinction seems mandatory and is explicitly considered in the present modeling principles.

Problems of associating fitness, and community fitness in particular, with adaptation become especially evident in statements like "Population fitness, or 'mean fitness of a population', perhaps surprisingly does not have a unique definition" in connection with "a population fitness-based definition of adaptation is too restrictive" (Kokko, 2021). Indeed, the absence of a clear definition of fitness cannot qualify it for providing an unambiguous notion of adaptation.

Whatever aspects of adaptation and its connection with community persistence are pursued, environmental and genetic diversity are inevitably involved. Utilization of environmental resources for reproduction in turn depends on modes according to which genetic diversity is distributed over environmental diversity and vice versa. Systems of migration provide the relevant mechanisms of distribution without which the implementation of adaptational processes remains unspecified.

Conditions for community persistence can thus be expected to decisively depend on specification of appropriate migration regimes, in addition to the modes according to which individual potentials for survival and reproduction (referred to as "expected fitness" by Brandon, 1995, p.10) are determined by genotype-environment associations. In the present paper, the dynamics of these associations, rather than their genetic and environmental components separately, are considered for their effects on community persistence. The relevant modeling details are introduced in the next section.

The interaction of the implied forces of adaptation takes place under the limitations set to reproduction by the capacities of environmental resources. Disregarding these density-regulating limitations would leave conclusions on the dynamics of community densities as the primary indicators of adaptation without substance. Moreover, with few exceptions, the utilization of resources implies reductions of their capacities, which need to recover in order to make utilization sustainable. Capacities of resources are therefore determined by their regenerative or replenishment capacities (as is implicit in MacArthur's (1970) seminal consumer-resource interactions model).

This however contrasts with frequently made assumptions in population genetic models of adaptation, where capacities of environments are viewed to determine fixed numbers of offspring contributed to the next generation (see e.g. Bolnick & Otto, 2013). One of the rationales behind these assumptions can be seen in the immigration-oriented (or "backward migration") approach, which is based on a posteriori (relative) frequencies of origins of residents within a location. The more comprehensive design of the present model requires migration regimes to be specified for what is known as "forward migration". A characteristic consequence of this mode of migration is that local community densities are dynamic and as such are the primary determinants of adaptational performance.

Successful adaptation of a community (whether a population or a species assemblage) to its environment is characterized by viable reproduction rates and sustainable

utilization of resources for reproduction. Sustainability implies that over-exploitation and possibly non-recoverable depletion of the resources is guarded against. Sustainable community densities can therefore be expected to be associated with the respectively extant resource capacities and to stay above certain threshold values, falling short of which is indication of extinction risk and thus adaptational failure. Regulation of utilization intensities of resources for reproduction as well as regulation of capacities of environmental resources is thus indispensable. Threshold values can be argued from different perspectives, among which is the probability of random extinction for low densities.

The contributions of evolutionary mechanisms acting via selection and migration on these regulations can thus be considered to play a central role in the assessment of adaptation. Since failure of adaptation is eventually a consequence of non-sustainable utilization of resources or of insufficient reproduction potential, ultimate community extinction is implied. This outcome has to be distinguished from the common notions of maladaptation as cited above. To our knowledge, attempts to model the drivers of adaptational community dynamics under the perspective of sustainable resource utilization seem to be rare, and this applies particularly to the role of migration (see e.g. Bolnick & Otto, 2013, for a partial exception).

Since the literature abounds with studies on selection-migration (balance) and related subjects (see e.g. the review of Tigano & Friesen, 2016), it is essential to consider the framing of our approach to the topic as outlined above. Our citation strategy follows this framing by referring to several reviews for purposes of general integration of contents and otherwise is confined to directly relevant literature. The work of Tomasini & Peischl (2020) is, however, to be mentioned, since it comes closer to the ideas on adaptation concerned with community persistence and migration among selectively diverse environments that are developed here.

The present treatment is not yet aimed at the presentation of theorems on specific aspects but rather at drawing broader, elemental conclusions from the relevant transition equations. Answers to some of the most obvious questions implied by these conclusions are provided with the help of specially designed scenarios and their numerical analyses. The modeling strategy is built on first developing the full model for genetic variation in reproduction norms (see Table 1) and migration regimes, considering that regulation of densities and resource capacities takes place in and belongs to the characteristics of each environment (see Figure 1). In the next steps, the model is detailed so as to allow verification of results obtained from established approaches of the kind recalled above.

Among the details is the absence of density and capacity regulation, since it is frequently focused on "relative" fitness. It is therefore not explicitly concerned with dynamics of population sizes or densities, and – as the "classic evolutionary view" – it is consequently restricted to the dynamics of relative genotype frequencies (see e.g. Brady et al., 2019, p.496). It is emphasized, however, that the adaptational significance of this view can be made explicit by turning from relative to absolute fitnesses and extending local regulation of density and capacity to regulation at the community level.

The questions of primary concern are: How does migration affect adaptation of the community to the density- and capacity-regulating factors of its environment? Can migration prevent or enhance the risk of resource loss with its implication of local or entire community extinction? How is genetic polymorphism involved in these adaptational processes?

2 General model specifications

Our modeling approach focuses on the principle effects of the adaptationally relevant system components in order to enable analysis, the results of which are not obscured by *a priori* interactions between the components. This seems meaningful, since analysis of interaction effects is based on knowledge of the effects of the involved individual components. The following specifications are therefore guided by this focus.

Therefore, the fitness (number of offspring, reproductive output) of a community member depends on its genetic type and on the environment to which it is exposed but not on the other individuals. Environments provide resources for reproduction that can be utilized to different degrees by different genotypes. Reproduction takes place by genetic self-replication, and offspring migrate or are dispersed to the available environmental conditions (forward migration). Note that the assumption of self-replication applies equally well to members of a population and members of a species assemblage.

Each member of the community is characterized by its genotype g, by the environmental conditions e affecting its reproductive potential over its lifetime, by its (potential) reproduction rate r, and by the (forward) migration regimes m of its offspring. Individuals do not modify each other's reproductive potential, which excludes community-internal effects from the environmental factors.

Reproduction potentials in different environments are conceived to be determined by an individual's genotype, which entails consideration of *norms of reaction for reproduction potential as the heritable information of genotypes* (for more notational details and terminology see Table 1). The environments among which migration occurs are the same as those that affect reproduction and optionally its density regulation and the regulation of resource capacities. In the following, a set of genotypes, their reproduction norms, and their migration regimes will be addressed as *a strategy of adaption* (or adaptational strategy) to the environmental conditions that are referenced by the reproduction norms and migration regimes. The present modeling principle follows the idea that such a strategy can be considered to be the more successful, the more of the environmental resources can be sustainably converted into reproduction.

The assumption of genetic self-replication serves the aim to elaborate the intrinsic effects of inheritance on the dynamics of the adaptational system. For the same reason, community sizes are assumed to be effectively infinite, so as to exclude interference of the intrinsic effects with causally undefined random events. Therefore, threshold values for community density are relevant to indicate that inferences based on the assumption of effective infinity become increasingly unreliable below the threshold.

The notion of environment is allowed to address various appropriate entities, such as resource, location, or habitat (for the relevant factors characterizing the entities see Table 1). This extension is useful when questions or problems of persistence not

Table 1: Glossary

g: genotype – heritable information of an individual or more general organismic entity.

e: environment – a set of external factors that determine the reproductive potential of individuals during their lifetimes, provide the resources for reproduction, are locations of residence and migration, and are determinants of regulation of local densities and resource capacities. The sum of these factors can be referred to as habitat.

Model parameters →

$r(g, e)$: potential reproduction rate (fitness) of g in environment e. For any genotype, the set of reproduction rates assigned to the environments to which it can be exposed is termed the *reproduction norm of reaction* of this genotype (*sensu* Woltereck, 1909; also see Sarkar, 1999, for a review).

$m(g, e, e')$: probability that an offspring of genotype g produced in parental environment e moves to environment e' ($\sum_{e'} m(g, e, e') = 1$, forward migration) – hence, for each genotype g, the matrix $m(g, \cdot, \cdot)$ is stochastic (transition matrix of a Markov-chain).

Model variables →

$p(g, e)$: joint frequency of combinations $g \times e$ (or probability that an individual has genotype g and inhabits environment e).

$p(g) := \sum_e p(g, e)$ and $p(e) := \sum_g p(g, e)$ denote the corresponding (marginal) frequencies of genotypes and environments.

$p'(g, e)$: joint frequency of $g \times e$ in the next (offspring) generation.

$\bar{r} :=$ average (absolute) fitness or multiplication rate of the community.

$c(e) :=$ resource capacity of environment e for reproduction measured in terms of supported community density at location e.

$d(e) :=$ community density at location e before reproduction.

$D := \sum_e d(e)$ or total community density.

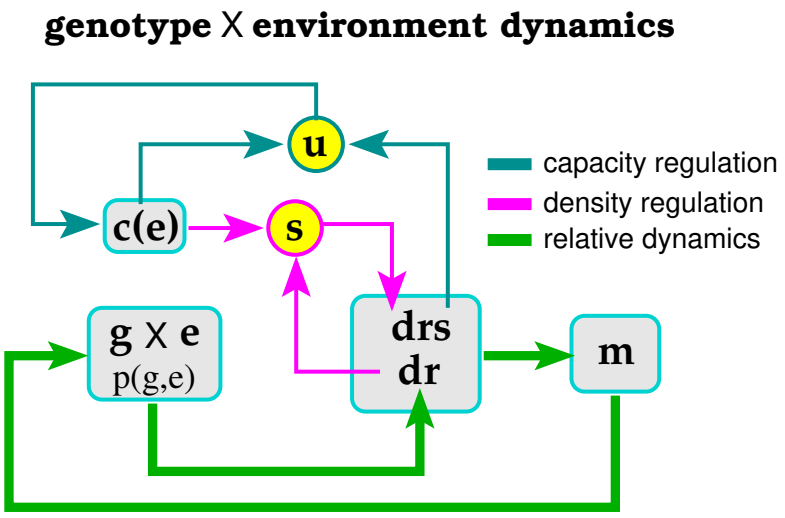
$d_r(e) := d(e) \cdot \sum_g r(g, e) \cdot p(g, e)/p(e)$ or reproduction density at location e prior to density regulation (potential reproduction).

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only of genotypes but also of environments are taken into account in any of these specifications as well as associations between the two. The entities will be used interchangeably whenever convenient. Environmental dynamics are conceived in terms of changes in occupation of environmental entities rather than alterations of environmental characteristics. The latter changes can be regarded to be included in the former in that migration may either be extended to reach existing conditions that were not targeted before, or individuals may have the potential to migrate to environments in which they were initially not represented.

In order to allow proper distinction between effects of (genetic) selection and migration on adaptational processes, migrational processes are assumed to have no effect on individual fitness. By this it is implied that genotype distributions which are realized before migration are not affected by migration. Differential preferences of migrants or dispersers for destination environments are, however, not excluded by this assumption.

Fig. 1 Flow diagram of the genotype×environment dynamics and the regulation dynamics of the model: $p(g,e)$ = relative frequency of a $g \times e$ association, d_r = potential reproduction density, d_{rs} = regulated reproduction density, m = migration regime, $c(e)$ = resource capacity of environment e, s = density regulation function, u = capacity regulation function.



Moreover, it is assumed that genotypes do not modify each other's fitnesses, as in the case of social interactions. This may give the impression that the present model does not explicitly cover community extinction that is due to what is commonly termed "evolutionary suicide". In fact, one of the suicide ideas is based on interactions resulting from invasion of a genetic type that has fitness below persistence levels and reduces the fitness of the originally viable resident types below its own fitness (for a review see Parvinen, 2005). Yet, the suicide problem will be returned to later with a different kind of explanation and causation that relates to the evolution of unsustainable utilization of resources.

2.1 Density regulation

Density regulation is commonly associated with the notion of "resource capacity" of environments, where the capacity is specified in terms of a maximum number of individuals that can be supported sustainably. A more suitable and comprehensive reference to resource capacity is probably in terms of the amount of energy provided by an environment for performing vital functions including reproduction. Accordingly, amounts of energy consumption in an environment are proportional to the number of resident individuals and the investment of energy per individual into survival and reproduction. Modes of density regulation are then concerned with the harmonization of energy provision and energy consumption.

On the community (global) and on the environmental (local) level the densities are D and $d(e)$, respectively (see Table 1). Herewith, $d(e)$ refers to densities before reproduction (including survival) and can therefore alternatively be addressed as the

density of immigrants into environment e plus stationary individuals (which stay at or return to their places of birth). In fact, the ratio between immigrants and stationaries specifies the connectedness of the location with the remaining community as mediated by migration. It lays the local basis for the community's adaptational process.

The amount of potential energy consumption in environment e with $d(e)$ initial residents then equals $d_r(e) = d(e) \cdot \sum_g r(g,e) \cdot p(g,e)/p(e)$ (see Table 1). Since $d(e) = D \cdot p(e)$, this consumption becomes $d_r(e) = D \cdot \sum_g r(g,e) \cdot p(g,e)$, which, in terms of density, specifies the overall potential number of offspring producible by the individuals present in environment e.

Consider the resource capacity $c(e)$ of environment e as the conversion of the energy it provides into numbers (density) of individuals, so that $c(e)$ can be conceived as the local density of individuals supportable by the environment. Density regulation then draws on the relation between potential and supportable local densities $d_r(e)$ and $c(e)$, so that density regulation can be regarded as a function s of $c(e)$ and $d_r(e)$, i.e. $s = s(c(e), d_r(e))$.

> From intuitive reasoning, one expects density potentials $d_r(e)$ to be realized to a large extent if they stay below the environment's resource capacity $c(e)$. Exceedance of the capacity then leads to stronger reductions in reproduction potential. This would show in s-values close to one at the outset and would continue with values that decrease more distinctly as $d_r(e)$ exceeds $c(e)$. Examples of such functions s are provided in the Appendix.

It might be apt at this point to mention that the above treatment of resource capacities accords with common concepts such as those characterized by the Verhulst differential equation of population dynamics and its extension to multiple agents in Lotka-Volterra form. Especially the latter form, in its version applied to consumer-resource interactions by MacArthur (1970, detailed in Chesson, 1990), is relevant in our model. As in previous work, resource capacity is again considered as a quantity of a resource of specified quality associated with a special environment.

The present representation differs, however, since it requires consideration of effects of resource capacities on community densities as indicators of adaptation and migration. Moreover, resources can be permanently available at a specified level, such as solar radiation or an artesian spring, or they are of dynamic (regenerative) kind. In ecosystem contexts, for example, primary producers establish consumer-resource interactions with regenerating resources of limited capacities. The food chains based on these producers confirm the elementary significance of such resources.

The effect of density regulation s on reproduction and its rates can be specified from different perspectives, but most directly the effect can be described by the degree to which reproduction rates are reduced as density $d_r(e)$ increases. Alternatively, s can be conceived as the probability to survive to the stage in which the reproductive potential r is realized. In any case, s summarizes the essential density regulation features of the model. Since in the present model selection effects are restricted to reproduction in order to avoid confounding of adaptational forces, density regulation is assumed not to depend on the local genetic composition.

The effect of s on reducing local potential reproduction $d_r(e)$ requires $0 \leq s \leq 1$ with s approaching 1 as $d_r(e)$ approaches 0. For more details see Appendix. Hence, density regulation results in reduction of $d_r(e)$ to $d_{rs}(e) := d_r(e) \cdot s(c(e), d_r(e))$, which

specifies the contribution of environment e to the community density of the next generation. It will be addressed as local density whenever it cannot be confounded with $d(e)$.

2.2 Regulation of resource capacities

So far, resource capacities of environments were considered to be constant and not affected by the density of their residents. Resource capacities regulated reproduction but not vice versa. As emphasized above, this assumption needs modification if environments and the resources they supply are exploitable and regenerative. Their capacities can be lowered (down-regulated) by high demands via reproduction and could recover (up-regulated) when demands are low (for more details see Appendix). In addition, the energy supply of environments must be assumed to be intrinsically finite, which entails that regeneration will never exceed a maximum capacity $cm(e)$ which will be addressed as the environment's "carrying capacity".

Environments have a twofold function in that they regulate reproduction and capacity regeneration. *Both functions are thus considered as characteristics of the environment to which adaptation takes place.* Reproduction and density regulation can be argued to precede the regulation of capacity regeneration, as the latter reacts to the result of the former (for illustration see Figure 1). Since regulation of reproduction results in densities $d_{rs}(e) = d_r(e) \cdot s(c(e), d_r(e))$, one requires a capacity-regulating function u, say, which establishes a transition from current $c(e)$ to $c'(e)$ in the next generation that fulfills the following self-explanatory requirements: all transitions stay below $cm(e)$; for $c(e) \leq cm(e)$ and densities $d_{rs}(e)$ the resource capacity increases or decreases in the next generation according to whether $d_{rs}(e) < c(e)$ or $d_{rs}(e) > c(e)$, respectively; it equals $c(e)$ for $d_{rs}(e) = c(e)$; it decreases with increasing $d_{rs}(e)$ for each fixed $c(e) \leq cm(e)$.

Note that $d_{rs}(e) = c(e)$ describes the situation where reproductive density and capacity are at equilibrium. Here, the carrying capacities $cm(e)$ are model parameters, while the $c(e)$ and the $d_{rs}(e)$ are model variables.

With the notation $c'(e) = u(c(e), d_{rs}(e))$ for the transition equation, the above requirements can be formally stated as:

$c(e) \leq cm(e) \Rightarrow u(c(e), d_{rs}(e)) \leq cm(e)$ for all $d_{rs}(e)$,

$d_{rs}(e) < c(e) \Rightarrow u(c(e), d_{rs}(e)) > c(e)$ for $c(e) < cm(e)$ (up-regulation),

$d_{rs}(e) > c(e) \Rightarrow u(c(e), d_{rs}(e)) < c(e)$ (down-regulation),

$d_{rs}(e) = c(e) \Rightarrow u(c(e), d_{rs}(e)) = c(e)$, and

$d_{rs}(e)\uparrow \Rightarrow u(c(e), d_{rs}(e))\downarrow$ for each $c(e) \leq cm(e)$.

Obviously, the requirements in lines 2 and 3 already follow from the other three requirements. Examples of this kind of regulation function are provided in the Appendix.

3 The transition equations

The dynamics of genotype-environment associations, or the joint distribution of genotypes and environments, and thus their *co-evolution* (in a generalized sense), is now governed by reproduction (r) of genotypes (g) in their environments (e), and density regulation of reproduction (s) is followed by offspring moving (m) from the environments of their parents to other environments (e'). Joint representations of genotypes and environments are determined by the share (number) of individuals that carry the genotypes and reside in the environments, respectively. After migration, the representation of environments is determined by the numbers of individuals arriving in them (emigration-oriented or forward migration approach).

For reproduction by self-replication, this leads to the following transition equation for the joint genotype×environment distribution (for notation see Table 1):

$$p'(g,e') = \sum_e p(g,e) \cdot r(g,e) \cdot s(c(e), d_r(e)) \cdot m(g,e,e')/\bar{r} \tag{1}$$

where the average reproduction rate

$$\bar{r} = \sum_{g,e} p(g,e) \cdot r(g,e) \cdot s(c(e), d_r(e))$$

additionally serves as a normalization factor guaranteeing that the frequencies sum to 1.

To arrive at the transition for the community density D, consider that the contribution of environment e to the community density D' in the next generation amounts to $d_{rs}(e)$. Note that this quantity reflects the interaction between the adaptational strategy and the environment. Then,

$$D' = \sum_e d_{rs}(e) = \sum_e d_r(e) \cdot s(c(e), d_r(e)) = D \cdot \bar{r} \tag{2}$$

It might be tempting to expect that $d_{rs}(e)/D' = p'(e)$. However, this would ignore the effect of migration on $p'(e)$.

When in all environments, their resource capacities are realized so that $d_{rs}(e) = c(e)$, then $\sum_e c(e) = D'$. This suggests $\sum c(e)$ as an analogue to the community's resource capacity. Yet, realization of this community density does not imply that their resource capacities are reached in all environments.

As was already shown, the transition equation for the capacities $c(e)$ of the local environmental resources takes the form

$$c'(e) = u(c(e), d_{rs}(e)) \tag{3}$$

These three transitions completely describe the structural dynamics of the community.

A number of features of the transitions provide intuitively desirable information on drivers of the dynamics.

By summing equation (1) over e' one obtains

$$p'(g) = \sum_e p(g,e) \cdot r(g,e) \cdot s(c(e), d_r(e))/\bar{r} \qquad (1a)$$

Hence, $p'(g)$ is the frequency of genotype g after migration. Note that connections between genotypes are solely determined here by the average $\bar{r}$. This is a consequence of the assumption of reproductive independence among genotypes and self-replication.

The effect of the environment on the dynamics can be analyzed by considering the norm of reaction of each genotype with respect to its reproduction rates in the different environments ("reproduction norm" for short). These norms persist via their genotypes over time (generations) and in this sense establish potential selection regimes. Temporal variation in selection regimes would then require the introduction of new genotypes with new reaction norms.

Averages taken over the reproduction norm of a genotype according to its representations in the environments yield

$$\bar{r}(g) := \sum_e p(g,e) \cdot r(g,e) \cdot s(c(e), d_r(e))/p(g)$$

and they specify the genotype's potential reproduction rate. With the help of this notion, equation (1a) can be written in the simplified familiar form

$$p'(g) = p(g) \cdot \bar{r}(g)/\bar{r}, \text{ where } \bar{r} = \sum_g p(g) \cdot \bar{r}(g) \qquad (1b)$$

Hence, the frequency of a genotype increases or decreases as its reproduction rate exceeds or falls below the community reproduction rate, respectively. This observation is useful in studies on the maintenance of polymorphism. It implies that polymorphism is lost as the reproduction rate of individual genotypes persistently exceeds the community reproduction rate. In particular, if $\bar{r}(g)$ is constant for all g, then only genotypes with maximum average reproduction rates persist.

Consideration of the joint distributions of genotypes and environments suggests to also take note of the environmental analogue of the potential genotype reproduction rate, i.e. the potential reproduction rate of an environment e:

$$\begin{aligned} \bar{r}(e) &= s(c(e), d_r(e)) \cdot \textstyle\sum_g p(g,e) \cdot r(g,e)/p(e) \text{ with} \\ \bar{r} &= \textstyle\sum_e p(e) \cdot \bar{r}(e) = \sum_g p(g) \cdot \bar{r}(g) \end{aligned}$$

$\bar{r}(e)$ in fact consists of the local potential reproduction rate $\bar{r}_0(e) := \sum_g p(g,e) \cdot r(g,e)/p(e)$ after reduction by the local density regulation factor.

To distinguish the significance of migration within the frame set by the above transition equations, it is useful to think of it as ruling or organizing the ways in which the potentials laid down in the reproduction norms of the genotypes are realized. For example, if migration of a genotype can be directed preferentially to the environments

where it realizes high reproduction rates (termed "matching habitat choice" by Edelaar et. al., 2008), this could be beneficial for the persistence of the genotype. Yet, other genotypes may realize even higher reproduction rates if their norms allow for this and are supported by appropriate migrational preferences. As will be detailed later, these expectations may however be basically questioned by the regulatory forces which can assign a negative adaptational role to genotypes with high reproduction potentials.

In the following, the term "habitat choice" will be used to address individual tendencies to preferentially migrate to particular locations (habitats) depending on the locations of birth of the individuals or their genetic types or both. Matching or mismatching habitat choice then connects target habitats of migration with the reproduction rates realized there (according to the reproduction norms). Preferential migration to habitats of high or low reproduction potential corresponds to matching and mismatching habitat choice, respectively. For reasons of considering the counterintuitive term mismatching habitat choice, see the above-cited paper of Edelaar et al. (2008). In the following, it is shown that mismatching choices may indeed be adaptationally advantageous by guarding against resource depletion.

3.1 Density regulation at the (global) community level

The present mode of density regulation applies equally to all subsets of environments and in particular to the whole community. In this case, where density regulation is not active at the level of individual environments but only at the community level, all community members are indeed subject to the same regulation intensity s. Local resource capacities $c(e)$ do not exist, but local numbers of potential offspring $d_r(e)$ do. The total number d_r of offspring potentially producible by the community then equals $d_r = \sum_e d_r(e)$.

Hence, the $s(c(e), d_r(e))$ all become equal to $s(c, d_r)$. When inserted into equation (1), the s cancels out and the transition of the joint distribution of genotypes and environments is independent of regulatory forces. Yet, making use of $\bar{r}_0 = \sum_{g,e} p(g, e) \cdot r(g.e)$ (the potential multiplication rate), $\bar{r} = s(c, d_r) \cdot \bar{r}_0$ continues to be subject to regulatory forces. The transitions (2) for community density and (3) for resource capacity remain the same. Hence, while the dynamics of relative genotype-environment frequencies affect the adaptational process, there is no feedback.

This is an important observation in that it reveals the "classic evolutionary view" to obtain adaptational relevance by simply turning from relative to absolute fitnesses and considering the resulting multiplication rate and the associated community density dynamics to be guided by finite resources limiting reproduction. Evolution becomes ecological. For the present topic, consideration of regulation at the community level (or "global" regulation) opens opportunities for studying the adaptational significance of local versus global regulation, with special reference to effects of (de-)stabilizing adaptational dynamics.

Clad in terms of selection and adaptation, and considering that selection concepts are based on relative fitnesses producing relative frequencies, one concludes that density regulation at the community level implies that selection affects adaptation but adaptation does not affect selection. In other words, *selection is detached from adaptation*. Adaptational feedback requires local density regulation. One of the consequences

of this feature of global regulation is that over-exploitation by large community densities may drive the whole community to extinction for weak regulation. For local regulation, on the other hand, over-exploitation can be locally confined and thus allow other locations to persist. It thus appears that the same adaptational strategy *is more likely to be successful (escape community extinction) under local than under global regulation.*

4 Local extinction

For regulation at the local level, the primary adaptational processes take place within locations and their environmental conditions. Community adaptation is therefore governed by the dynamics of the local densities $d(e)$, which gives their persistence precedence.

Apparently, continuing immigration into a location would prevent local extinction if it would not elicit resource over-exploitation (i.e. $d_{rs}(e) > c(e)$) that was not present before immigration. Recall that perpetual over-exploitation implies perpetual resource capacity reduction and thus local community extinction via resource depletion. It therefore remains to identify further extinction risks in the absence of immigration and for possibly stable resource supply (absence of resource depletion).

Amounts of immigration can be determined by distinguishing among the residents those that were born in the location and stayed there (stationaries). For genotype g and location e, the respective probability is $m(g, e, e)$, and the associated density of stationaries (after density regulation) in the next generation is

$$d_{stat}(e) := d(e) \cdot \sum_g p(g, e) \cdot r(g, e) \cdot s(c(e), d_r(e)) \cdot m(g, e, e)/p(e)$$

Consequently, the density of immigrants in the next generation equals $d'(e) - d_{stat}(e)$, where $d'(e)$ is the value of $d(e)$ in the next generation. The fraction $f_{im}(e)$ of immigrants in this generation therefore equals

$$f_{im}(e) := (d'(e) - d_{stat}(e))/d'(e) = 1 - d_{stat}(e)/d'(e)$$

The contribution of stationary reproduction to the potential reproduction rate $\bar{r}'_0(e)$ in this generation then is $1 - f_{im}(e)$, so that $\bar{r}'_0(e) \cdot (1 - f_{im}(e))$ quantifies the *stationary potential reproduction rate* in environment e. If this rate is less than one, the stationary reproduction potential would be insufficient for persistence in the location. Note that *stationary reproduction potential strongly depends on local emigration rates.* Especially for high emigration rates, local reproduction may easily become insufficient.

Hence, if the local community persists despite such insufficiency, this must be due to stabilizing immigration. On the other hand, immigration would have a destabilizing effect if resource depletion would take place in the presence of insufficient stationary reproduction potential. In this case, immigration would have caused resource over-exploitation. Local extinction without resource depletion can then be caused by insufficient stationary reproduction potential and low fractions of immigration.

Stationary reproduction potential and its density regulation constitutes one of two basic adaptational components under local regulation. The other specifies the immigration effect on adaptation via mutual selection-immigration balances between locations. This will be treated in more detail in a later section.

For (global) regulation at the community level, extinction causes are either overall resource depletion or insufficient reproduction in the sense that $\bar{r} < 1$ prevails. Since no local regulation of the reproduction potentials of genotype-environment associations takes place, all of these associations compete for the same resource and thus increase the chances for selection of the most reproductive association and by this raise the risk of over-exploitation. In reverse, local regulation may cull these associations while retaining the others together with their local resources. The latter option establishes a coherence between selection and adaptation which is not realized for global regulation.

5 The combined effect of density and capacity regulation

As is shown above, there are two major threats to community persistence: over-exploitation of resources and insufficient stationary reproduction combined with low degrees of immigration. Both types of regulation, resource capacity and density as well as their interaction, are addressed here. In the following, the interaction will be featured.

Continually weak density regulation, where an excess of reproduction potential over resource capacity is not reduced below this capacity, will lead to ongoing down-regulation of the capacity and thus threaten resource and consequently local community persistence. This trend could be compensated by advancing resource regeneration (up-regulation of the capacity) during phases in which reproduction remains below the resource capacity. On the other hand, strong capacity down-regulation could potentially endanger resource persistence.

Especially for large reproduction potentials, strong capacity down-regulation perpetuates over-exploitation of resources for weak density regulation. In this way, *individual resources may become depleted due to repeated over-exploitation in combination with inadequate (weak) density regulation followed by capacity down-regulation.* This cannot be prevented by mitigation of capacity down-regulation without intensifying density regulation. Reducing only the capacity down-regulation may reduce the speed of resource depletion in the presence of inadequate density regulation.

For strong density regulation, where a potential reproduction excess over the current resource capacity is reduced below this capacity, resource persistence is temporarily not endangered. Indeed, each potential excess of the current capacity ($d_r(e) > c(e)$) could be followed by a reduction below the current capacity ($d_{rs}(e) < c(e)$, see regulation function $s1$ in the Appendix for an example), and the subsequent capacity regulation would allow for regeneration of the resource and thus enhance its capacity ($u(c(e), d_{rs}(e)) > c(e)$). In the next generation, either $d_r(e)$ remains below the increased capacity or will be reduced below that capacity. In both cases, the capacity will be further up-regulated.

However, the strength of density regulation could force the potential reproduction rate repeatedly below 1, implying ultimate community extinction. This is likely to go along with a decline of the regulated reproduction, which then stays below the current capacities with the result that these are up-regulated. Hence, *due to strong density regulation, local or entire community extinction may occur without resource depletion.*

In the absence of capacity regulation, weak density regulation generally has no adverse effects on community persistence, but this may change in the presence of capacity regulation. Conversely, strong density regulation may entail community extinction in the absence as well as in the presence of capacity regulation. Yet, the absence of capacity regulation probably is an unrealistic assumption.

More specifically, genotype-environment associations are at a reproductive disadvantage if their reproduction potentials are not regulated so as to avoid overexploitation of the concerned environment's resource capacities. Recurrent failure of such regulation would imply ongoing reduction of the resource's capacity. By this, the representation of the respective associations in the community as well as the sustainable community density would be lowered. Implied is the risk of depletion of the resource and thus the concerned associations altogether. *Selection therefore acts on genotype-environment associations according to their conformation with the environmental capacities and their regulation.*

These regulatory processes react to the reproduction potentials of the genotypes and their distributions over resources. Especially the latter are governed by the modes of migration prevailing in a community and by this determine the genotype-environment associations.

6 A different perspective on selection-migration balance

Each environment can be assigned a genotype that is the most reproductive in this environment among all genotypes and would thus tend towards local fixation under complete isolation. Local genetic polymorphism can therefore be considered to be the result of at least incomplete isolation, allowing individuals from other locations to immigrate and by this provide chances for establishing some kind of local *selection-immigration balance*. The balance can be realized by migration regimes of genotypes that differ in their local preferences.

In particular, if the locally superior genotype shows a migrational preference for this location (by this practicing matching habitat choice), then each other immigrating genotype, despite being at a disadvantage, may persist if it realizes a sufficient preference for migrating into this environment. All the more, the representation of the immigrant genotype grows with its migrational preference for the location.

Immigration therefore implies at least partial replacement of the reproductively superior genotype by inferior ones. This need not be an adaptational disadvantage, since local regulation of density and resource capacity could have caused resource overexploitation by the locally most reproductive genotype followed by resource depletion. Partial replacement of this genotype by reproductively inferior ones could thus avoid

over-exploitation and resource loss and by this convey an adaptational advantage to the community. This applies similarly to immigration that is not genetically directed.

From this perspective, the adaptational significance of *genetic polymorphism within environments as a reproduction-moderating and by this stabilizing force* becomes particularly evident. Local communities are thus rescued from extinction. Albeit, the supply with local genetic variation by immigration requires that this variation be maintained between environments.

Hence, maintenance of genetic variation *between* environments is necessary for realization of the locally stabilizing effect of genetic variation *within* environments (for the difference in perspective see e.g. Jasper & Yeaman, 2024). On the other hand, genetic variation within a location already indicates maintenance of genetic variation between locations with the consequence that selection-immigration balance by itself provides the mechanisms of maintaining polymorphism between locations. The adaptationally stabilizing effect of immigration may however also be realized through complete replacement by the reproductively inferior genotype, if the latter ultimately terminates a previous phase of over-exploitation by the reproductively superior genotype. In this case, the degree of immigration of a genotype must consistently exceed its degree of reproductive inferiority.

7 Elemental analysis of effects of migration

In this section, elemental conclusions which do not require detailed technical proof are inferred from the transition equations and their subsequent explanations. In accordance with the present topic, the conclusions will be directed towards specific effects of migration on the joint genotype-environment dynamics and the associated adaptational characteristics.

7.1 Density regulation at the community level: Absence of local regulation

(1) No migration (stationarity): $m(g, e, e') = 0$ for $e \neq e'$ ($m(g, e, e) = 1$). In this case, $p'(g, e) = p(g, e) \cdot r(g, e)/\bar{r}_0$, so that ultimately only pairs (g, e) with maximum rate of reproduction remain.

(2) No selection: in this case $r(g, e) = r$ and $p'(g, e') = \sum_e p(g, e) \cdot m(g, e, e')$. Summation over e' confirms that genotype frequencies remain constant over generations ($p'(g) = p(g)$), and the dynamics is limited to changes in representation of the environments of each genotype. This takes place independently for each genotype and of the multiplication rate $r \cdot s(c, D \cdot r)$ and thus the density dynamics of the community. The environmental dynamics is then completely defined by the structure of the (stochastic) transition matrix m (e.g. being irreducible or aperiodic with the implied convergence of the environmental distribution).

There are two conditional forms of the absence of selection:

(2*a*) All reproduction norms identical: $r(g,e) = r(e)$ for all g, $p'(g,e') = \sum_e p(g,e) \cdot r(e) \cdot m(g,e,e')/\bar{r}_0$, and summing over e' yields $p'(g) = \sum_e p(g,e) \cdot r(e)/\bar{r}_0$. Contradicting intuitive expectations, selection seems to take place, since p'(g) does not equal p(g).

(2*b*) Constant reproduction norms (pure genetic selection): $r(g,e) = r(g)$ for all e, $\bar{r}_0 = \sum_g p(g) \cdot r(g)$, $p'(g,e') = r(g) \cdot \sum_e p(g,e) \cdot m(g,e,e')/\bar{r}_0$ and $p'(g) = p(g) \cdot r(g)/\bar{r}_0$. The latter equation shows that migration has no effect on genotype dynamics and that ultimately only genotypes with maximum reproduction rate persist. The environmental dynamics is then governed by the migration matrices of the remaining genotypes.

(3) Migration of offspring independent of genotype and parental environment (termed *neutral migration* in the following): $m(g,e,e') = m(e')$, so that from equations (1) and (1a) $p'(g,e') = p'(g) \cdot m(e')$ with $\sum_{e'} m(e') = 1$ and $p'(e') = m(e')$. Thus, after the first generation $\bar{r}(g) = \sum_e r(g,e) \cdot m(e)$ is constant for all g, and by the remark following equation (1b), ultimately only genotypes with maximum reproduction rate $\bar{r}(g)$ of their reproduction norms remain in the community.

In summary, genetic polymorphism cannot be maintained in the absence of migration (case (1)), in the absence of environmental effects on the reproduction rates of genotypes (case (2b)) independently of the migration regime, nor for independence of migration from genotype and parental environment (neutral migration, case (3)). In case (1) only special combinations of genotype and environment remain, which does not apply to cases (2b) and (3). For purely environmental (non-genetic) selection (case (2a)), genetically variable migration regimes can effect changes in genotype and environmental frequencies. It is worth emphasizing here that *not only initially present genotypes but also initially represented environments as well as individual genotype-environment associations can ultimately vanish as the result of special migration regimes.*

These elemental results for the model without local regulation suggest that *differential migration in the sense of depending on genotype or parental environment (non-neutral migration) is necessary for the maintenance of genetic polymorphism; migration has no effect on the dynamics of genotype frequencies if reproduction does not depend on environment.* Moreover, loss of polymorphism is governed by selection processes that head towards genotypes and environments that realize current maximum reproduction rates. Yet, even in the absence of genetic variability, environmental dynamics may continue due to the migration regime and the reproduction norm.

Beyond this, however, it is conceivable that loss of genetic polymorphism lowers community reproduction rates to the degree that the migration regimes of the remaining genetic variants may imply the continuing settling of environments in which reproduction rates for these variants are reduced. Mechanisms that maintain genotypes which do not realize the maximum overall reproduction rate in any environment may therefore lead to better utilization of environmental resources of limited capacity and by this be beneficial to community survival.

Particularly case (1) may cause confusion, since it states that all community members ultimately show the same genotype and reside in the same environmental condition. This could support the reasonable expectation of overcrowding of a single resource and would suggest that it must go along with a sizable reduction of community size, probably ending with community extinction. Such deliberations require consideration of regulatory forces.

7.2 Density regulation without capacity regulation

(1) Global versus local density regulation: All of the results obtained above for global regulation apply to local density regulation. The new aspect of global regulation now entering the analysis solely concerns problems of effects of the internal dynamics on the dynamics of community density, with particular focus on conditions for community extinction. The relevant variable is the community multiplication rate $\bar{r} = s(c, d_r) \cdot \bar{r}_0$. Reductions in $\bar{r}_0$ close to 1 thus are crucial, and this can be supported by "mismatching habitat choice", where genotypes tend to preferentially migrate to environments in which they do not realize their maximum potential reproduction rates.

(2) Isolated environment (absence of immigration into environment e', i.e. $m(g, e, e') = 0$ for $e \neq e'$): One obtains in this case $p'(g, e') = p(g, e') \cdot r(g, e') \cdot s(c(e'), d_r(e'))/\bar{r}$. Consider two genotypes of which g_1 has maximum potential reproduction rate among all genotypes in e', so that for any inferior genotype g_2, $r(g_2, e')/r(g_1, e') < 1$ holds. Thus, since s does not depend on genotype, it cancels out, yielding

$$\frac{p'(g_2, e')}{p'(g_1, e')} = \frac{p(g_2, e')}{p(g_1, e')} \cdot \frac{r(g_2, e')}{r(g_1, e')} < \frac{p(g_2, e')}{p(g_1, e')}$$

for global as well as local density regulation, so that the quotient $p(g_2, e')/p(g_1, e')$ and thus $p(g_2, e')$ tend to zero over the generations. The reason is that the strict inequality applies to all initial frequencies in the sequence. Therefore, the genotype inferior within e' ultimately vanishes within this environment. Since this applies to all inferior genotypes, one concludes that in the absence of immigration into an environment ultimately only genotypes with the same maximum potential reproduction rate in this environment remain there. This makes sense even if the respective environment vanishes asymptotically.

If immigration takes place into none of the environments so that migration is effectively absent altogether, then ultimately in each environment essentially a single genotype with its unique potential reproduction rate remains. In this case, density regulation at the local level guards against extinction, so that in the different environments different genotypes can prevail if initially present. Contrasting with global regulation, genetic polymorphism thus can persist. Typically, its distributions over environments are characterized by the absence of diversity within environments and high diversity between them. This characterization of the environmental distribution of genetic polymorphism is standard in much of ecological and population genetic work on adaptive differentiation. Yet, even small amounts of continuing immigration could substantially increase the genetic diversity within locations.

(3) Neutral migration ($m(g,e,e') \equiv m(e')$): From equation (1) one obtains $p'(g,e') = p(g) \cdot \bar{r}(g) \cdot m(e')/\bar{r} = p'(g) \cdot m(e')$, and by summation over g, $p'(e') = m(e')$. Hence, $p'(g,e') = p'(g) \cdot p'(e')$, so that after the first generation $p(g,e) = p(g) \cdot p(e)$ always holds. It follows that $\bar{r}(g) = \sum_e m(e) \cdot r(g,e) \cdot s(c(e), d_r(e))$. Unlike case (3) for the absence of local regulation, $\bar{r}(g)$ is not constant due to the variability of s among the environments, so that the previous conclusions about genetic polymorphism do not unconditionally apply for density regulation at the local level. In one of the scenarios presented later, it indeed turns out that polymorphism may persist under local density regulation.

At least for consistent superiority of potential reproduction rates between genotypes, i.e. where $r(g_2,e) < r(g_1,e)$ in all environments e, however, one obtains $\bar{r}(g_1) - \bar{r}(g_2) = \sum_e m(e) \cdot (r(g_1,e) \cdot s(c(e), d_r(e)) - r(g_2,e) \cdot s(c(e), d_r(e))) = \sum_e m(e) \cdot (r(g_1,e) - r(g_2,e)) \cdot s(c(e), d_r(e))$, since $d_r(e)$ does not depend on genotype. Hence, $\bar{r}(g_1) > \bar{r}(g_2)$ and $p'(g_2)/p'(g_1) = (\bar{r}(g_2)/\bar{r}(g_1)) \cdot (p(g_2)/p(g_1)) < p(g_2)/p(g_1)$. For the same reasons quoted in the above case (2), the inferior genotype g_2 therefore cannot persist irrespective of the kind of density regulation at the local level. This applies to all genotypes persistently inferior to any other genotype. As a result, if more than one genotype persists, then all of these show genotype×environment interaction for reproduction, i.e. for no two genotypes is the ranking of their norms of reaction consistent. Maintenance of genetic polymorphism is commonly associated with this phenomenon.

(4) When dropping all restrictions on migration regimes, generally valid results on the maintenance of genetic polymorphisms may not hold even under the considerably more stringent assumption of total superiority for potential reproduction rates between genotypes. The reason is that $\min_e r(g_1,e) > \max_e r(g_2,e)$ need not imply that also $\min_e r(g_1,e) \cdot s(c(e), d_r(e)) > \max_e r(g_2,e) \cdot s(c(e), d_r(e))$. Moreover, it is conceivable that extreme mismatching habitat choice for at least one genotype may stabilize the genetic polymorphism, probably at the risk of community extinction.

7.3 Density and capacity regulation

None of the elemental results obtained for the model without capacity regulation is invalidated by the introduction of capacity regulation. The reason is that all of these statements can either be inferred without having to consider density regulation, or at least density regulation is involved and by this complicates certain conclusions. The latter are not simplified by capacity regulation. Yet, for completely isolated environments, in which the most reproductive genotype tends towards fixation, capacity regulation may imply depletion of the environmental resource as a consequence of over-exploitation.

As indicated above, for sufficiently strong density regulation, a positive feedback loop may result that leads to ever increasing resource capacities approaching the upper bounds $cm(e)$. Since this takes place irrespective of the strength of capacity regulation, of the reproduction potentials as well as of the migration regimes, the ultimate dynamics would follow the lead set by the model without capacity regulation.

Especially the extinction risk resulting from weak density regulation followed by resource depletion calls for forces that could lower this risk. Among these are first of

all migration strategies that preferably send individuals to environments where their reproduction is suboptimal (mismatching habitat choice). Local density $d(e)$ may then decrease and may therefore add to lowering the reproduction yield below the current capacity. Resource regeneration could then start again. This topic will be further explained and detailed with the help of two scenarios presented in the following section.

So far, the above deliberations support a concept of adaptation that is oriented at a community's potentials for sustainable utilization of environmental resources, including their heterogeneity. Ultimately, utilization is unsustainable and adaptation has failed if communities go extinct. Yet, such failure can be restricted to individual environments implying local extinctions that do not imperil community persistence altogether. It may however entail sustainable community densities at a lower level. Herewith it is important to consider the fact that *extinction refers to groups of individuals (at local or entire community levels) and may have two basic causes, resource depletion resulting in resource loss, and inability to realize viable rates (≥ 1) of (stationary) reproduction (insufficient reproduction).* In the latter case, resources may persist while local communities go extinct.

8 Model scenarios

The following scenarios are intended to take up some of the more significant problems indicated and left unsolved by the above elemental analysis of the adaptational significance of migration. Special emphasis is given to the two domains mentioned at the end of the introduction. Herewith, use will be made of the fact that the adaptational significance of the "classic evolutionary view" (focusing on relative frequency dynamics) can be perceived by distinguishing between density and capacity regulation acting at the global and at the local level. By this it is possible to treat density and capacity regulation at both levels for their adaptational dynamics. This will be done in each of the scenarios.

In order to guarantee comparability of the results obtained for the two levels of regulation, the same adaptational strategies and the same regulation functions are applied (i.e. the model parameters are the same). With respect to the maximum capacities, this requires that $cm = \sum_e cm(e)$. In addition, the initial values of the model variables are also set equal, where in particular $c = \sum_e c(e)$.

Among the model parameters characterizing the environment, several variants of the intensity of density regulation are considered. Parameters of resource capacity regulation will not be varied in this paper, since this regulation type addresses a distinct quality of environmental control (see above) and in order to keep the analyses coherent. For density regulation, the focus is on the strength of "above-c" regulation, where reproduction potentials exceed the resource capacity ($d_r > c$) and over-exploitation of resources ($d_{rs} > c$) may deplete resources, followed by local or entire community extinction.

8.1 Two scenarios: "Habitat choice" and "habitat fragmentation"

The following two recurrently addressed types of scenarios, "habitat choice" and "habitat fragmentation", treat elementary roles that migration can play for adaptation in concert with reproduction potentials and modes of regulation.

Fragmentation is most simply characterized by the interplay between local isolation (or stationarity) and spreading among locations. The environmental conditions of the locations determine both the reproduction potentials of the genotypes (via their reproduction norms) and the modes of regulation of density and resource capacities. Distribution by way of migration over the environmental conditions then determines the realization of the reproduction potentials, where degrees of fragmentation are closely associated with the degree of local isolation versus degrees of neutral dispersal. The scenario will focus on the effects of these degrees on adaptational success and the role of genetic polymorphism under different regulation intensities.

The adaptational relevance of habitat choice, in turn, is determined by the reproduction potential a genotype acquires in the "chosen" habitat. Common perception suggests that a genotype's choice would be advantageous if migration is directed to habitats allowing for maximal reproduction of the genotype (a matching habitat choice), while otherwise (a mismatching choice) this should be disadvantageous for both the genotype's and the community's reproduction rate. Yet, under density and capacity regulation neither one nor the other type of habitat choice alone might safeguard resource and community persistence. The potential adaptational dominance of migration over selection will be demonstrated by considering selection regimes that suggest clear selective inferiority of one genotype over another.

So far, the above deliberations and explanations suggest that the initially stated view of adaptation be the basis for interpretation of the observations made below. This view is characterized by considering reproduction norms and migration regimes as strategies of adaption of a community to a variable environment that involves density and capacity regulation functions as essential components. Such strategies can be rated to be the more successful, the more of the environmental resources they sustainably convert into reproduction (without over-exploitation). In the following scenarios, local community extinctions or depletion of local resources will therefore be counted as partial adaptational failure that diminishes the community's overall adaptational performance. Along the same line, fluctuating density dynamics may be considered as the result of imperfect adaptation (not to be mistaken as maladaptation or adaptational failure), since it can be expected to result from strong above-c density regulation in connection with continuing over-exploitation of the resource.

Preliminary numerical tests of the model suggested that scenarios with two genotypes and three environments suffice to demonstrate the model's basic potential for discerning adaptational characteristics of migration regimes when acting on environmental diversity distinguished by density- and capacity-regulating forces. For density and capacity regulation functions, we refer to $s1$ and u, respectively, as specified in the Appendix.

9 Scenario I: "Habitat choice"

The description (characterization, delineation) of habitat choice and its special version, argued above to be of particular interest in the present context of adaptation, is reflected in the choice of parameters specified in Table 2. In particular, genotype g_1 is totally superior to genotype g_2 in reproduction. The superior genotype practices mismatching habitat choice, thus lowering its reproductive potential, while the inferior genotype enhances its reproductive potential by practicing matching habitat choice. Four sub-scenarios were chosen with the focus on the adaptational significance of the intensity of density regulation for reproduction, while holding the degree of resource capacity regulation constant.

The four sub-scenarios Scenario I(a)–I(d) illustrated in Figs. 2–5 are based on the same adaptational strategy and initial densities (see Table 2). The first three begin with the same initial joint frequencies as listed, the same capacity regulation parameters $ub = uh = 1.0$, and the same density regulation parameters $sa = 0.1$, $sb = 0.5$. They differ only by the above-c density regulation parameter sh. The fourth sub-scenario is the same as the first except for the initial joint frequencies.

Each figure illustrates the success of the adaptational strategy in Tab. 2 under regulation over the course of up to 100 generations, where the above-c density regulation sh is either weak (Figs. 2,5), medial (Fig. 3), or strong (Fig. 4). Of the five panels, the uppermost three marked e=1 to e=3 show the results of local regulation within that location. Of the three graphs within each panel, the top graph plots the local density $d_{rs}(e)$ after density regulation (light blue) and the local resource capacity $c(e)$ (red); the dotted line marks the maximum capacity $cm(e)$. The middle graph shows the immigration rate $\bar{r}'_0(d)\cdot f_{im}(e)$ (dark green) and the stationarity rate $\bar{r}'_0(e)\cdot(1-f_{im}(e))$ (light green); the dotted white line marks the level 1. The bottom graph shows the relative frequencies of genotype g_1 (dark blue) and genotype g_2 (yellow) in location e. In the fourth panel of local regulation, the upper graph shows the community density $D = \sum_e d(e)$ (light blue) and the sum of local capacities $\sum_e c(e)$), and the lower graph shows the relative frequencies of g_1 (dark blue) and g_2 (yellow) in the community as a whole. The fifth panel shows these two graphs for global regulation. If graphing in a panel terminates before completion of the 100 generations, the density has fallen below the threshold of 0.00001, indicating extinction. Otherwise, the location or the community persists for at least 100 generations.

▷ *Interpretation of Scenario I(a) (Fig. 2):* With the adaptive strategy and initial frequencies specified in Tab. 2, the community cannot adapt to a weak density-regulating environment and becomes extinct within a few generations.

Local regulation: All three locations become extinct. The two locations e=1 and e=3 whose reproductive potential is raised by strong immigration rapidly become extinct through over-exploitation. In location e=3 with the highest reproduction rate for both genotypes, the weakly regulated reproductive potential exceeds the capacity $c(3)$, forcing it and the density $d_{rs}(3)$ downwards to 0. The extinction of e=1 through over-exploitation from the same forces lags ca. two generations behind. e=2 becomes extinct simultaneously with e=3 through insufficient reproduction caused by cessation of immigration and low stationary reproduction due to high local emigration rates

Fig. 2 Scenario I(a): "Habitat Choice" for weak above-c density regulation sh=0.5 over 100 generations for local regulation in locations e=1 through e=3 and the entire community, then for global regulation in the community

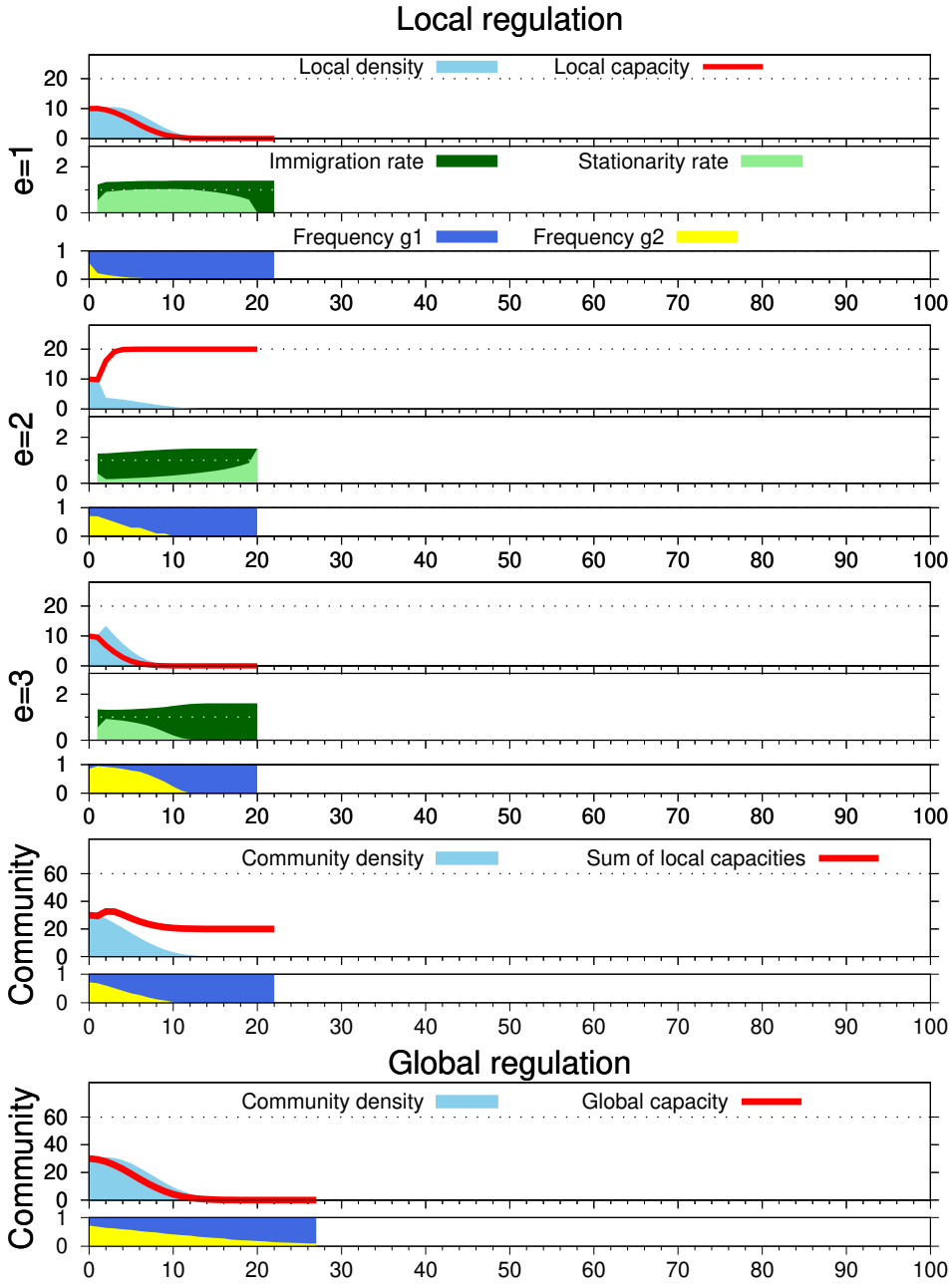


Table 2: Scenario I "Habitat choice". The initial joint frequencies are chosen such that the reproductively inferior genotype is given a starting advantage. This is motivated by the intuitive expectation that otherwise the inferior genotype would experience a two-fold disadvantage driving it *a priori* to extinction.

		e=1	e=2	e=3	
Adaptational strategy (parameter values)					
Norms of reaction	$r(g_1, e)$	1.4	1.5	1.6	unconditionally superior
	$r(g_2, e)$	1.1	1.2	1.3	unconditionally inferior
Migration regimes	$m(g_1, \cdot, e)$	0.8	0.1	0.1	mismatching
	$m(g_2, \cdot, e)$	0.1	0.1	0.8	matching
Initial variable values					
Initial joint frequencies	$p(g_1, e)$	3/21	2/21	1/21	(dark blue)
	$p(g_2, e)$	4/21	5/21	6/21	(yellow)
Initial densities	$d(e)$	10	10	10	(light blue)

(0.9, implying a stationary reproduction rate $\ll 1$). As opposed to resource depletion in e=3 and e=1, the low density in e=2 allows regeneration of its resource capacity.

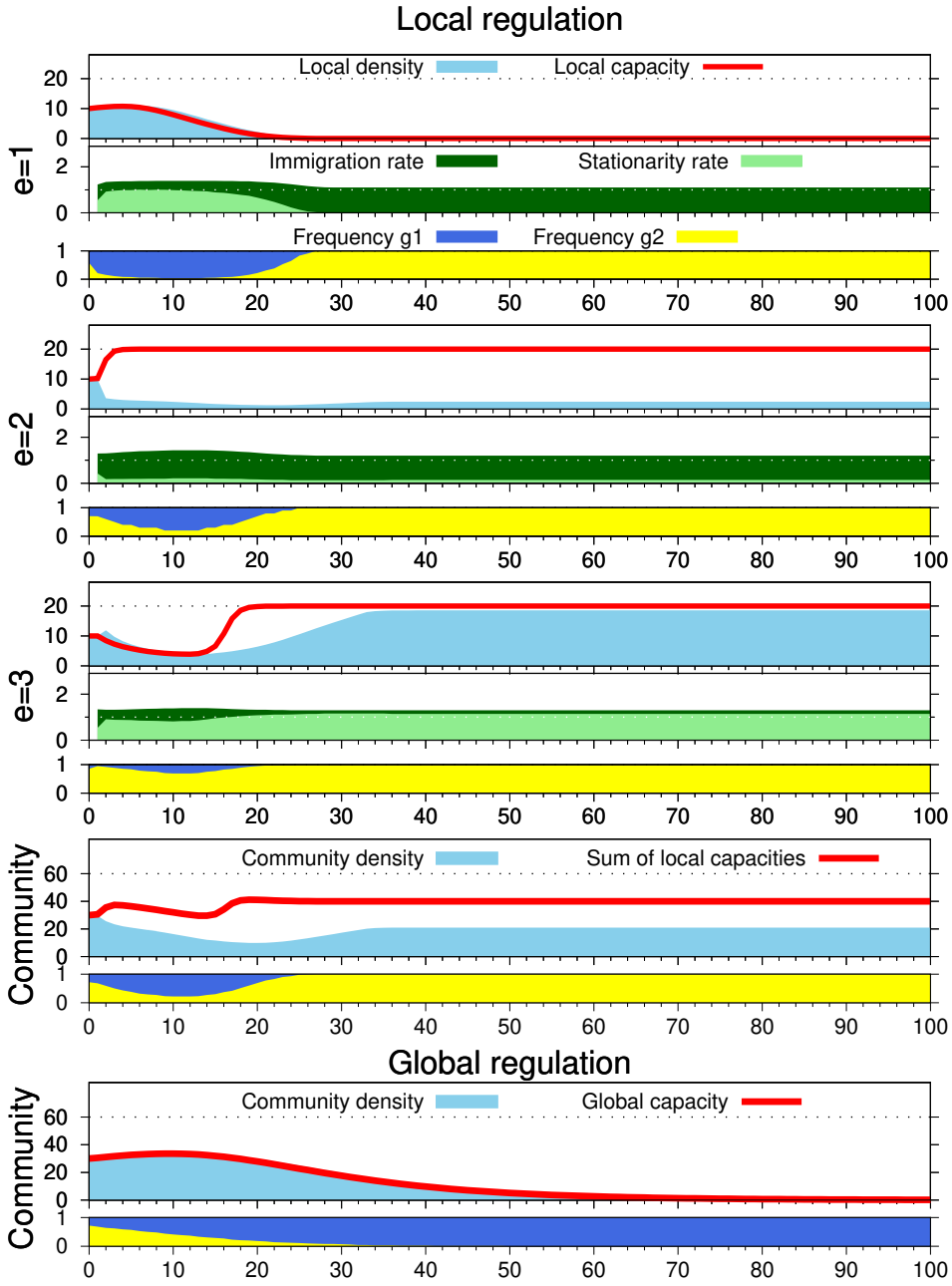
In all locations before extinction, the fitter genotype g_1 approaches fixation instead of the initially more frequent genotype g_2. In e=1, g_1 quickly approaches fixation due to its higher reproduction rate and its high preference for this location. In e=3, g_2 persists longer due to its higher initial frequency, its high preference for e=3, and the low preference of g_1 for e=3, but it cannot compensate for the higher reproduction rate of g_1, especially since the faster decrease of its density $d_{rs}(3)$ raises the relative density of immigrants from e=1, most of which are of genotype g_1. In e=2, fixation to g_1 results from the higher reproduction rate of g_1 and the decreased immigration of g_2 from the declining e=3.

Global regulation: Adaptational failure is caused by over-exploitation of the common resource; insufficient reproduction plays no role unlike for local regulation. When extinction is reached, the community is still polymorphic but on its way to fixation of the fitter genotype g_1.

▷ *Interpretation of Scenario I(b) (Fig. 3):* For moderately weak density regulation, the adaptive strategy maintains two of the three locations under local regulation, but adaptation fails under global regulation.

Local regulation: Location e=1 tends toward resource depletion as in I(a), indicating over-exploitation, but in e=3 the local community persists after a short inititial decline. As e=3 declines, however, regulation is strong enough to reduce reproduction below the capacity, which recovers, reversing the tendency toward depletion and stabilizing the local density just below the maximum capacity due to sufficient stationary reproduction. For the migrationally least preferred location e=2, the small stationarity rate ($\ll 1$) is augmented by sufficient immigration from e=3 to allow its capacity to recover and hold the density stable at a low level. Thus, location e=2 is essentially maintained by immigration, and its resource is maintained at maximum capacity. The fact that in e=3 a very small contribution of immigration persists, suggests a small

Fig. 3 Scenario I(b): "Habitat choice" for moderately weak above-c density regulation sh=0.65 over 100 generations for local regulation in locations e=1 through e=3 and the entire community, then for global regulation in the community density regulation sh=0.65



amount of immigration which can only originate from e=2. In all locations, the less reproductive genotype g_2 becomes fixed, due to the extinction of location e=1 preferred by genotype g_1. There is no effective selection-immigration balance realized among the persisting locations, as follows from the loss of genetic polymorphism despite persistence of two locations. Actually, one location persists due to sufficient stationary reproduction in e=3 adjusted by low local emigration rates (0.2) from this location and indicated by a high stationarity rate. Location e=2 is simply maintained by the low amounts of emigration from e=3.

Global regulation: The community maintains a seemingly stable increasing capacity over a few generations, but it is approached from below and finally exceeded by the density. This pushes the capacity towards depletion and the density towards 0, indicating over-exploitation.

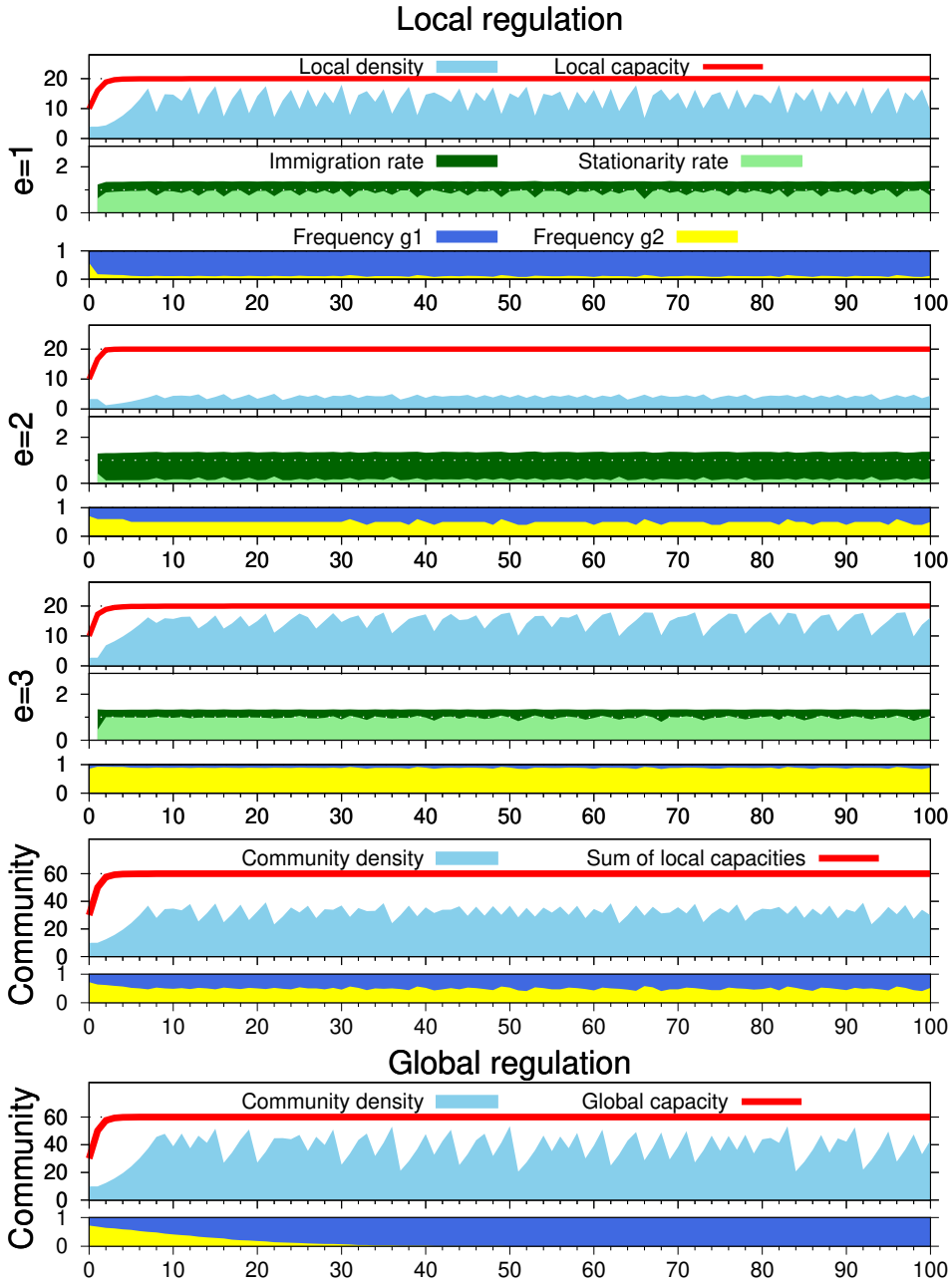
Hence, while for local regulation the community persists at reduced but stable density, community persistence is threatened in the long run for global regulation. This reflects the above general characterization of the difference in adaptational dynamics between local and global regulation by which fixation of the most reproductive genotype-environment association is promoted for global regulation. Apparently, this association entails over-exploitation. Indeed, on its way to extinction, the fitter genotype g_1 steadily increases. It is this genotype which also elicits resource depletion in environment e=1 under local regulation and by this supports fixation of the less fit genotype g_2.

It is interesting to note that the dynamics for local regulation indicates a situation of *evolutionary rescue*. In fact, the initial invasion of the reproductively superior genotype g_1 goes along with a density decline which is counteracted later on along with an increase of the reproductively inferior genotype g_2. The rescue here is owed to the genotype that avoids over-exploitation by reducing its reproduction potential and realizing sufficient stationary reproduction. Although the U-shaped density dynamics agrees with the "hallmark of evolutionary rescue" stated in Figure 1 of the paper of Carlson et al. (2014), its present causes oppose those listed by the authors (as well as in the comprehensive review of Uecker et al., 2026) in that the genotype that is superior in fitness endangers community persistence and the inferior genotype guards against this fate.

In contrast, for global regulation, the same adaptational strategy implies *evolutionary suicide*, since initially the presence of the reproductively inferior genotype confers an adaptational advantage to the community which, however, is destroyed by the subsequent increase of the reproductively superior genotype with its persistent over-exploitation of the resource, leading to community extinction. This is probably one of the most startling examples of contrast between the adaptational effects of local and global regulation, since the *evolutionary rescue achieved under local regulation turns into evolutionary suicide under global regulation.*

▷ *Interpretation of Scenario I(c) (Fig. 4):* For strong regulation, the adaptive strategy maintains all three locations under local regulation and the community under global regulation. In each case, the capacity quickly increases towards its maximum, indicating that regulation persistently and strictly prevented over-exploitation.

Fig. 4 Scenario I(c): "Habitat choice" for strong above-c density regulation sh=5.0 over 100 generations for local regulation in locations e=1 through e=3 and the entire community, then for global regulation in the community



Local regulation: The densities in all locations fluctuate between generations but remain distinctly above the extinction threshold and below the capacity, which becomes maximal. Fluctuations in e=1 and e=3 are initiated by a sharp reduction in density every time the reproduction exceeds the capacity, which is maximal. Reproduction is then allowed to increase over one or more generations until it again becomes excessive, and the density follows. The fluctuations do not seem to follow a pattern and may even be chaotic. In location e=2, persistent immigration of both genotypes from e=1 and e=3, though fluctuating in frequency, prevents extinction as would otherwise impend because of insufficient stationary reproduction (with rate $\ll 1$). Genotypes g_1 and g_2 are nearly fixed in their preferred location e=1 and e=3, respectively. In each of the two locations, the genotype that does not prefer the location immigrates at low frequency. In e=2, both genotypes immigrate at fluctuating but nearly equal frequency, establishing a stable polymorphism. This accords well with the general explanations on selection-migration balance and especially with reference to genetic variation within and between locations.

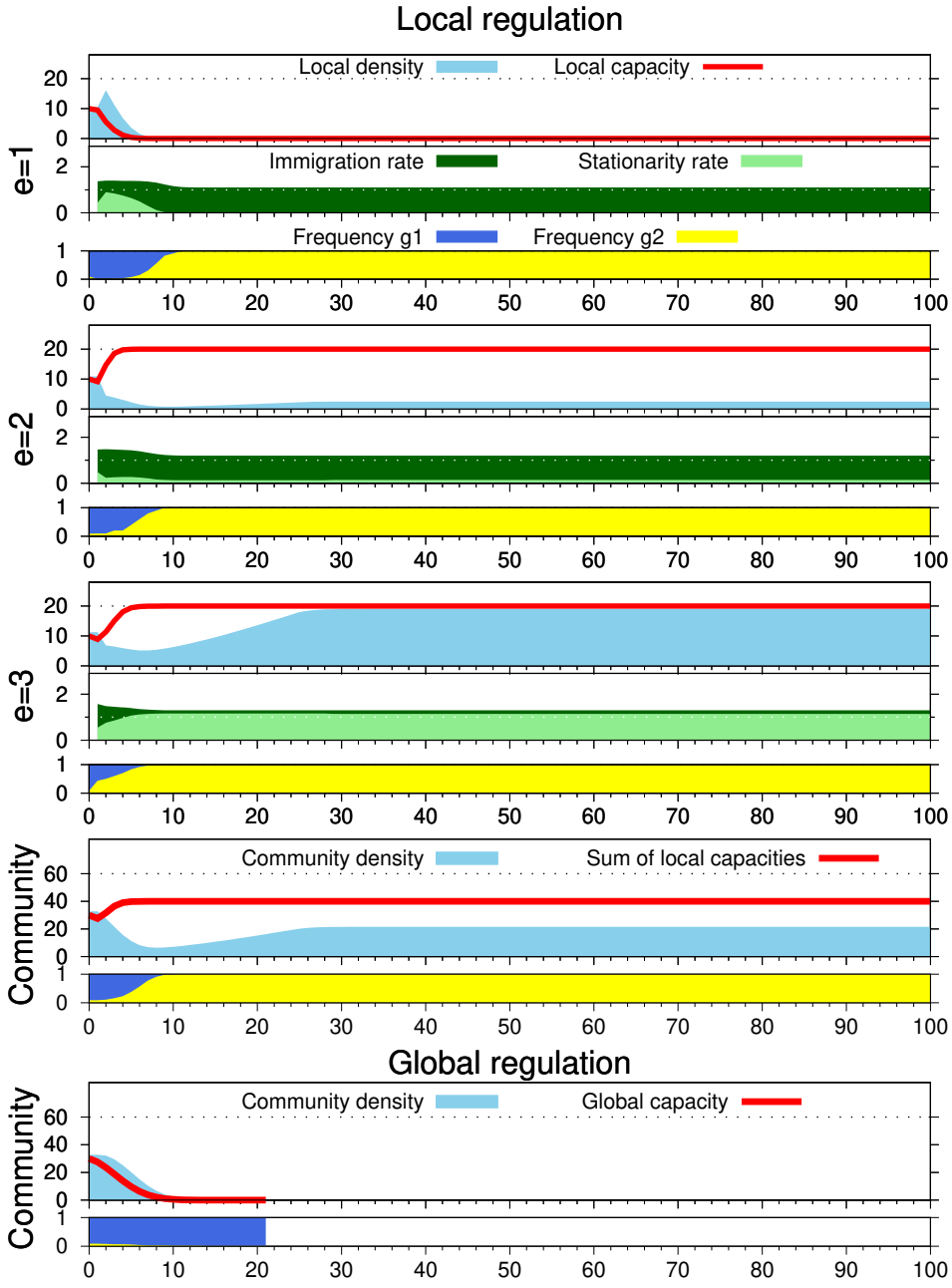
Global regulation: The range of density fluctuations is wider in both directions. Contrasting with local regulation, polymorphism is lost, and total fixation takes place to the fitter genotype g_1. Hence, the potential for over-exploitation is maximal and is most drastically reduced by strong density regulation. This explains the enhanced fluctuations at this level of regulation.

By evading resource depletion, strong density regulation apparently allows the community's adaptive strategy to convert more of the environmental resources effectively into reproduction and, by this, to persist at higher average densities. At first sight, this seems to contradict the repeated strong reductions in reproductive potential by density regulation. It yet becomes plausible when considering that the reductions increase the chances for resource regeneration, allowing the capacities to quickly tend toward their maxima. In particular, this applies to more environments and thus leads to a broader reproduction basis. On the other hand, this gain is paid for by marked imperfection in adaptation. This is even more pronounced for regulation at the global level, suggesting that local regulation decreases adaptational imperfection.

Since the above results do not support the expectation that larger initial frequency of the reproductively inferior genotype has a compensating effect, it was checked provisionally whether the general adaptational tendencies may be affected by the initial frequencies. For this purpose, we tried the other extreme, where the reproductively inferior genotype additionally starts with a lower frequency. It turned out that this did not affect the long-term adaptational tendencies for moderately weak and strong above-c density regulation. This holds for both levels of regulation, local and global. For weak regulation, however, the picture changed as documented in the following Fig. 5.

▷ *Interpretation of Scenario I(d) (Fig. 5):* The major insight from this scenario consists in the observation that, *for weak density regulation, adaptation may take opposite routes depending solely on the initial frequencies.* For regulation at the local level, the two extremes of community extinction and community persistence may result. Notably, persistence is achieved via fixation of the reproductively inferior genotype, thus counteracting tendencies of over-exploitation in the location e=3. In scenario I(a), however,

Fig. 5 Scenario I(d): "Habitat choice" for weak above-c density regulation and low initial frequency of the inferior genotype over 100 generations for local regulation in locations e=1 through e=3 and the entire community, then for global regulation in the community



the reproductively superior genotype takes over with the consequence of increasing over-exploitation to a degree leading to community extinction. Hence, the lower initial frequency of the reproductively inferior genotype provides the reproductively superior genotype with a starting advantage that entails a phase of over-exploitation that is temporary in e=3 but lasting in e=1. Apparently, the ultimate dynamics is very similar to that in scenario I(b) with its stronger regulation intensity. The explanations offered there thus apply. In contrast, at the global level of regulation, community persistence is prohibited independently of the inititial conditions due to over-exploitation by the reproductively superior genotype. Again, making use of popular terminology, the present scenario shows tendencies of evolutionary rescue (the U-shaped community density dynamics under local regulation), but now enabled by a change in the initial conditions.

9.1 Synopsis of "Habitat choice"

The following statements refer to the adaptational strategy detailed in Table 2. It is noticeable that in all cases of community persistence under local regulation, the reproductively inferior genotype is maintained and even prevails in the community. The location that is least preferred by all genotypes entails insufficient stationary reproduction and is therefore maintained essentially by immigration. Apparently, the applied migration regime largely overrides the tendencies suggested by the selection potentials. Selection potentials are thus modified not only by density regulation, which is jointly determined by local density and resource capacity. Local densities in turn are strongly affected by the migration regime. This realizes selection effects that may markedly differ from the original selection potentials laid down in the reproduction norms of the genotypes. It is reminiscent of classical forms of density-dependent selection but differs basically at least through the introduction of migration and the combination of density regulation of reproduction and capacity regulation of resources.

Adaptation and community persistence is then governed by events of resource over-exploitation or by insufficient stationary reproduction. The strength of density regulation seems to be decisive here, in that sufficiently strong regulation may prevent genotypes from over-exploitation to the degree allowing for a stable genetic polymorphism with its stabilizing selection-migration balances. This contrasts with global regulation, where in all cases the reproductively superior genotype tends towards fixation, with the consequence that, for moderately weak and weaker density regulation, over-exploitation drives the community to extinction. This confirms the above suggestion about the adaptational difference between global and local regulation. With increasing weakness of local density regulation, community extinction proceeds from facultative (depending on initial conditions) to unconditional.

10 Scenario II: "Habitat fragmentation"

Referring to the above general description, the migrational basis of fragmentation is now characterized by a proportion α of individuals that stay at their locations of birth while the remainder practices neutral migration. The migration matrix can thus be specified as a mixture in proportions α and $1 - \alpha$ of two matrices, the former

Table 3: Scenario II "Habitat fragmentation". The initial joint frequencies are all set equal, in order to get clues about the direction into which the adaptational strategies send the dynamics.

		e=1	e=2	e=3	
Adaptational strategy (parameter values)					
Norms of reaction	$r(g_1, e)$	2.3	2.0	1.7	genotype×environment-interaction
	$r(g_2, e)$	1.8	2.1	2.2	
Migration	$m(\cdot, e, e')$	$\alpha \cdot \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix} + (1-\alpha) \cdot \begin{pmatrix} 0.3 & 0.4 & 0.3 \\ 0.3 & 0.4 & 0.3 \\ 0.3 & 0.4 & 0.3 \end{pmatrix}$			
Initial variable values					
Initial joint frequencies	$p(g_1, e)$	1/6	1/6	1/6	(dark blue)
	$p(g_2, e)$	1/6	1/6	1/6	(yellow)
Initial densities	$d(e)$	10	10	10	(light blue)

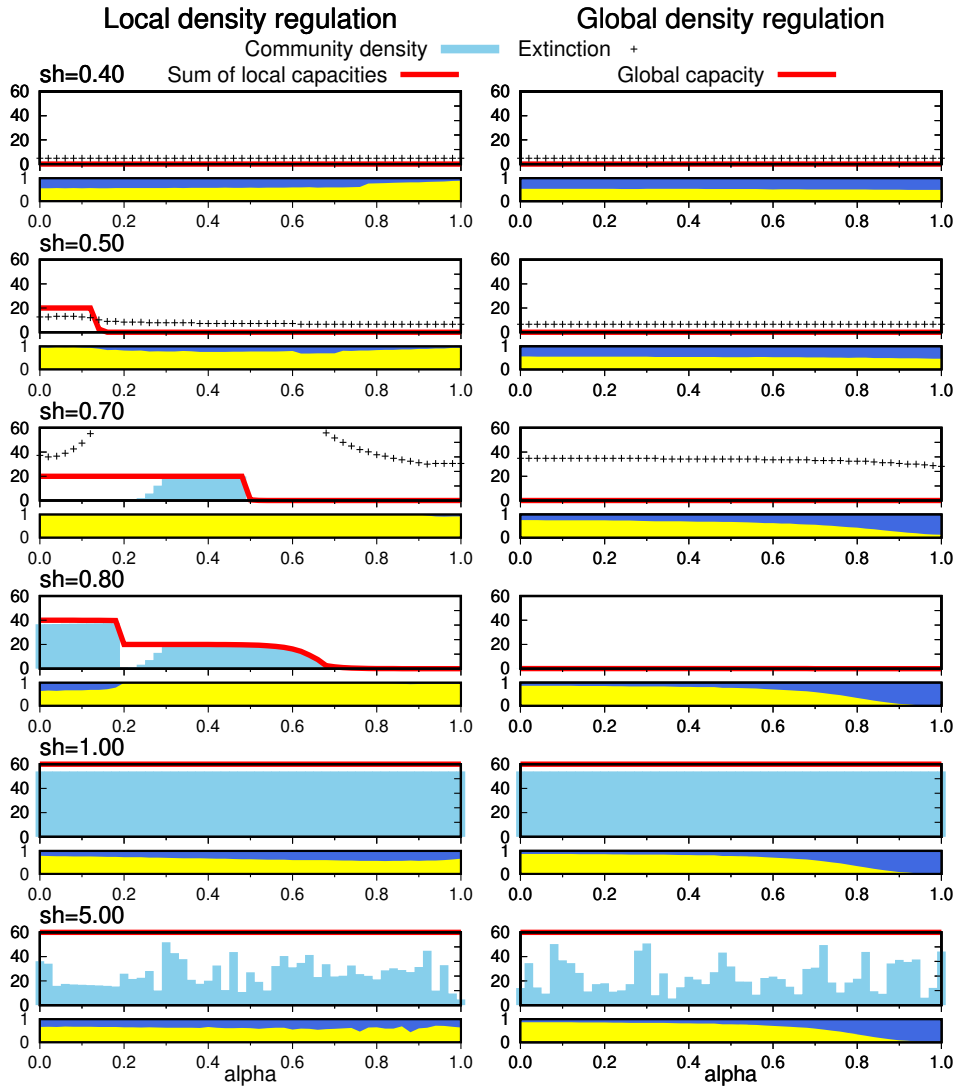
representing the stationary and the latter the neutral migrational behavior. As opposed to Scenario I of habitat choice, genotypes are now assumed to not affect this behavior (for the resulting adaptational strategy see Table 3). α can be conceived as the degree of fragmentation of the community. The specific effects of migration on adaptation then become apparent along the degrees of fragmentation.

To cover this fragmentation spectrum (for $0 \leq \alpha \leq 1$), we performed an inspection of α-effects on the community densities and resource dynamics at the state after 100 generations under the adaptational strategy and initial conditions specified in Table 3. By this we obtained an overall idea of the long-term effects on the adaptational process. Motivated by the apparent significance of density regulation suggested by the study of Scenario I, we considered the long-term effects for several density regulation intensities sh along the α spectrum to get an impression about how degree of fragmentation and intensity of density regulation interact in the adaptational dynamics. This is done by plotting community density, sum of local capacities, and genotype frequencies against α for each of a number of sh-values (see Fig. 6). The resulting information suffices for inference of the number of persisting locations, distinguishing extinction causes with respect to resource depletion and insufficient reproduction as well as the participation of genetic polymorphism in these events. Adjacent plots show the local level of regulation (left) and the corresponding global level (right).

Interpretation of the graphs in Fig. 6:

Local regulation (left column):
▷ Highly fragmented communities (large α): Weak (sh=0.4, 0.5) or moderately weak (sh=0.7, 0.8) density regulation leads to resource depletion ($c(e)$=0) and extinction ($d(e)$=0) through over-exploitation in all environments. • For strong regulation (sh=1.0, 5.0), the community persists in all environments with resource capacities approaching their maxima ($d(e) \leq c(e)$=$cm(e)$).
▷ Slightly fragmented communities (small α): Weak to moderate density regulation sh=0.4, 0.5, 0.7 entails community extinction, but overall resource depletion is limited

Fig. 6 Scenario II: "Habitat fragmentation" for several above-c density regulation intensities sh. In generation 100 for the fragmentation scenario (Tab. 3), community density, sum of local resource capacities, global capacity, and genetic polymorphism are plotted as functions of the level of regulation (local or global), the intensity of density regulation (sh), and the degree of fragmentation (α). The left column of graphs shows local density regulation, the right column global regulation. Both graphs on a line result from the same degree (sh) of density regulation, ranging from weak (sh=0.4) (top) to strong (sh=5.0) (bottom). Within each graph, the variable α on the x-axis designates the migration regime, ranging from the absence of fragmentation ("neutrality", α=0) to complete fragmentation ("complete local isolation", α=1). A "+" above a degree of fragmentation α signifies extinction of the respective community in the generation indicated on the right-hand y-axis, scaled 0 to 100.



to very weak regulation (0.4). For sh=0.5, 0.7 we found (not shown) that depletion takes place in e=1 and e=2, causing cessation of immigration into e=3. The insufficient stationary reproduction potential realized in e=3 then implies local extinction without resource depletion. • Higher density regulation sh=0.8 causes depletion in e=2. By this, immigration into e=1 and e=3 is reduced and therefore allows these two locations to avoid over-exploitation by mutual selection-immigration balance and thus to fully utilize the two resources at maximum capacity of $cm(1) + cm(3)$=40. The balance is maintained by persisting genetic polymorphism. It is interesting that persistence is suddenly strongly reduced for fragmentation around α=0.2: both resources e=1 and e=2 deplete, stopping immigration into e=3. Insufficient stationary reproduction potential realized in e=3 then pushes $d(3) \downarrow 0$ but allows $c(3)$ to assume its maximum of $cm(3)$=20.

▷ Medially fragmented communities (intermediate α values): Weak density regulation sh=0.4, 0.5 cannot prevent resource depletion by over-exploitation in all locations. • For sh=0.7, 0.8, resources e=1 and e=2 deplete by over-exploitation, while resource e=3 persists at maximum capacity $c(3)$=20. Mutual selection-immigration balance fails here (and the genetic polymorphism vanishes), but stationary reproduction potential in the environment e=3 is adapted with genotype g_2 to the degree of density regulation without immigration. Cessation of immigration thus bans the risk of over-exploitation in e=3. This explains the possibly surprising observation that moderately weak density regulation sh=0.7, 0.8 ensures community persistence under medial fragmentation.

▷ All degrees of community fragmentation under strong density regulation ($sh \geq 1$): For sh=1, all locations persist, and their densities are close to the maximum resource capacities. As regulation sh increases to 2, we observed (not shown) decreasing densities while maintaining "perfect adaptation". • For $sh > 2$, all locations persist, but the densities begin to fluctuate seemingly chaotically within the open interval between 0 and maximum capacity in all environments and in their sum, not only between generations ("imperfect adaptation") but also between neighboring α. In any case, selection-immigration balances are realized, as is apparent from persisting genetic polymorphism. At the other extreme, under weak density regulation (sh=0.4, 0.5), community extinction eventually resulted for all degrees of fragmentation as a consequence of resource depletion. Only for small *alpha* and less weak regulation (sh=0.5) did resource depletion not take place in one location.

Global regulation (right column):

▷ All degrees of community fragmentation: For weak regulation ($sh < 1$), over-exploitation occurs in all environments, leading to depletion of all resources and extinction of the community. • For sh=1, all environments persist at the same maximum density D'=54 as for local regulation, and the resources are maximal at SUM(cm) = 60 for all degrees α of fragmentation. • For strong density regulation sh up to 2, the density converges stably to a value below the maximum for sh=1 and the resources to their maximum of cm=60 for all α ("perfect adaptation"). • For even stronger density regulation $sh > 2$, the community persists and resources remain maximal, but the overly strong regulation produces seemingly chaotic density fluctuations between generations and between neighboring α within the interval between 0

and maximum capacity ("imperfect adaptation"). With increasing fragmentation and regulation intensity, the genotype with the maximum overall reproduction potential increases. This is in accordance with the fact that for high degrees of local isolation, the genotype-environment association with highest reproduction potential increasingly dominates the dynamics. The density fluctuation appears stronger for global than for local regulation across the fragmentation degrees, in that more situations come close to extinction thresholds in the former.

10.1 Synopsis of "Habitat fragmentation"

The following statements refer to the adaptational strategy detailed in Table 3. The reproduction norms show genotype-environment interaction, which implies that genotypes realize their maximal reproduction potentials in different environments, a condition which is generally considered to support the maintenance of genetic polymorphism.

For local regulation, community adaptation to weakly density-regulating environments failed for all degrees of fragmentation, and it was incomplete for all degrees of fragmentation under strong density regulation. To moderately weak regulation, adaptation was possible, however only for special degrees of fragmentation, with slight changes in these degrees suddenly leading to adaptational failure. An especially odd situation occurred for moderate-to strong regulation (sh=0.8), where fragmentation degrees leading to situations close to extinction are flanked on both sides by degrees allowing community persistence. Here, one resource went to depletion while the other two persisted due to mutual selection-immigration balance for low fragmentation.

In another case, selection immigration balance failed and one resource persisted due to sufficient stationary reproduction achieved by adjusted local emigration rates, as determined by the degree of fragmentation. Adaptation to environments that are moderately weakly density-regulating is therefore very sensitive to small modifications in adaptational strategy. For global regulation, in turn, options for adaptation to a fragmented habitat are even limited to a strong density-regulating environment and are characterized there by dynamics that are quite similar to local density regulation (concerning both perfect and imperfect adaptation). It thus appears that weak density regulation may provide a substantial challenge for adaptation to fragmented habitats, and this is especially hard to overcome for density regulation at the global level.

11 Concluding remarks

The most noticeable lesson to be taken from the present model and confirmed by the two scenarios is that migration can reverse selection effects and density regulation can reverse adaptational tendencies, and that this is rather the rule than the exception in adaptational processes. Driving forces are individual habitat preferences in the first case and resource over-exploitation in the second, where the latter is always imminent when potential reproduction rates exceed 1. Rates below 1 rule out persistence from the outset. For rates above 1, over-exploitation impends and thus regularly requires density regulation to reduce the menace of resource depletion. Mechanisms supporting

adaptation are therefore concerned with reducing over-exploitation to a degree that enables the regulatory forces of the environment to prevent resource depletion.

Among these mechanisms, individual habitat choice, coupling migration preferences with local reproduction rates, takes a prominent position with its potential to counteract over-exploitation. The weaker the density-regulating effect of the environment, the fewer are the chances of adaptational success by counteracting over-exploitation. Since for local regulation, tendencies for maximization of reproductive success prevail under isolation, immigration of reproductively inferior genetic types from other locations is required to mitigate excessive local reproduction. This is one of the principles of selection-migration balance. Mechanisms for maintaining inter-local genetic polymorphism are thus vital to prevent resource depletion.

These mechanisms operate by mutual selection-immigration balance among locations. Otherwise, if selection-immigration balance fails (with resource depletion implied), stationary reproduction potentials and their local regulation gain adaptational momentum. Adjustments of local emigration rates as parts of the adaptational strategy are crucial here. From this perspective, maintenance of mutual selection-immigration balance and sufficient stationary reproduction potentials appear as the major components of adaptation. Herewith, selection-migration balances among locations can blend into persistence that is chiefly supported by sufficiency of stationary reproduction at individual locations. In these cases, persistence can be extended to several locations, maintained solely by immigration but mostly at low density levels, as is demonstrated in scenarios I(b) and I(d) of habitat choice.

The fragmentation scenario clearly demonstrates the high consistency of effects of density regulation on adaptation, where across all degrees of fragmentation, low degrees of local and especially global regulation caused community extinction. For strong density regulation, community persistence is accompanied by pronounced density fluctuations, again across all fragmentation degrees. These fluctuations come close to the extinction threshold, especially under global density regulation.

In the habitat choice scenario, on the other hand, the genetic effects on migration can provide additional means of escaping the dominating effects of density regulation that characterize the fragmentation scenario. This applies to both extremes of density regulation.

If density regulation takes place at the global community level, the outcome of selection processes (which determine the relative dynamics of genotype-environment associations) are not affected by regulation forces, while the community density is. As a consequence and as compared to local regulation, global regulation offers fewer adaptational options due to the lack of local confinement of over-exploitation. The latter provides additional chances for adaptation via the less reproductive environments which are not in danger of over-exploitation. These locations in turn may contribute to the establishment of selection-immigration balances at other locations.

Moreover, our scenarios confirmed the expectation that for local regulation, maintenance of genetic polymorphism is more readily achieved and helps reduce the risk of resource depletion, especially for weak density regulation. For strong regulation, the extinction risk is replaced by the risk of increasing adaptational imperfection. From

this perspective, the same adaptational strategy is likely to be more successful under local than under global density regulation.

To prevent misconception, it should be recalled that sustainable utilization of resources, in the sense that resources persist, does not *per se* rule out local or global extinction of communities. The cause can be found in the principle difference that must be made between local persistence due to immigration from other locations and local persistence due to reproduction that is not exported (is stationary). Especially as the result of large emigration rates, it may occur that stationary reproduction does not suffice for local persistence despite sizeable reproduction potentials. Local persistence can then be upheld only by immigration. Otherwise, local community extinction would proceed while local resources persist. This can be considered as another significant effect of migration on adaptation that is closely associated with local densities governed by immigration.

So far, deliberations on the adaptational significance of density regulation have been given preference over capacity regulation. As indicated in our provisional explanations, this can be questioned when the interplay of sensitivities to reproduction between density and capacity regulation becomes more complex. We feel, however, that the present results on density regulation provide a useful preparation for more directed analysis to follow.

12 Appendix: Regulation functions

12.1 Density regulation *s*

For convenience set $q = d_r/c$, where d_r and c retain the above meaning of potential offspring density (after reproduction) and resource capacity, respectively. Suppose that if $q > 1$ and the capacity c is exceeded, then s should trim d_r below c, i.e. $d_r \cdot s(c, d_r) = d_{rs}(c, d_r) < c$, or equivalently $s(c, d_r) < 1/q$. This condition in combination with the requirement that $s(c, d_r)$ decreases with increasing d_r conforms with the interpretation of c as a resource capacity. It applies to situations where capacities are not allowed to be exceeded, which would establish a quite strong mode of density regulation.

The probably simplest shape for s that obeys the above requirements is

$$s(c, d_r) = \begin{cases} 1 - q \cdot sa & 0 \le q \le 1 \\ (1 - sa)/q & q \ge 1 \end{cases}$$

where $0 \le sa \le 1$. Strength of regulation increases here with increasing parameter sa simultaneously below and above capacity. Regulation control can be more refined by adding two parameters sb and sh as exponents of q:

$$s1(c, d_r) = \begin{cases} 1 - q^{sb} \cdot sa & 0 \le q \le 1 \\ (1 - sa)/q^{sh} & q \ge 1 \end{cases}$$

where $sb, sh \ge 0$. Regulation can be strengthened below resource capacity by decreasing sb, and the same can be achieved above capacity by increasing sh. For reasons of continuity and to prevent ambiguous and unrealistic results, $s1(0, d_r) = 0$ is postulated. Simultaneous regulation above and below capacity by changes in sa remain the same as before. Note that $sa = 1$ implies depletion of the environmental resource if

d_r does not stay below the capacity c of the environment. Moreover, for $sa = 0$, d_r is not regulated below the capacity while above-capacity regulation remains active.

Smoother shapes for s can be derived from the following accordingly normalized version of Richards's (growth) curves (Richards, 1959) when applied to appropriate choices of parameters $a, b, h \geq 0$. The implied regulation characteristics are less stringent than in the previous example in that they prevent reduction within a single step from above to below the capacity.

$$s2(c, d_r) = \left(\frac{h + \exp(-a)}{h + \exp(a \cdot (q - 1))} \right)^b$$

As before, and for the same reasons, $s2(0, d_r) = 0$. The effects of the parameters on $s2$ can more generally be evaluated by considering that $s2$ decreases with increasing a, with decreasing h, and with increasing b. The condition that reduction in density be moderate at densities below the capacity ($q < 1$) and increase distinctly above the capacity ($q > 1$) is realized e.g. for $a = 50$, $h = 1$, and $b = 0.1$. Note that the condition cannot be fulfilled for $h = 0$, since then $s2(c, d_r) = \exp(-a \cdot b \cdot q)$ and s becomes a strictly convex function of q. Moreover, the choice of parameters reflecting the difference between regulation characteristics below and above capacity is less apparent in $s2$ than in $s1$.

12.2 Regulation u of resource capacity

The following example takes up the principle underlying the density regulation function $s1$ given in the previous section and applies it to regulation characteristics of capacities of environments.

$$c' = u(c, d_{rs}) = \begin{cases} cm - (cm - c) \cdot (d_{rs}/c)^{ub} & \text{for } \mathrm{d_{rs}} \leq \mathrm{c} > 0 \\ c \cdot (c/d_{rs})^{uh} & \text{for } \mathrm{d_{rs}} \geq \mathrm{c} \end{cases}$$

with $ub, uh \geq 0$. In accordance with the requirements, $u(c, d_{rs})$ decreases with increasing d_{rs}, $u(c, d_{rs}) = c$ for $d_{rs} = c$, and $u(c, d_{rs}) \leq cm$ for $c \leq cm$. For reasons of continuity, $u(0, d_{rs}) = 0$ for all d_{rs}. As before, u allows for separate regulation below and above capacity, again with stronger up-regulation (below capacity) by increasing ub, and stronger down-regulation (above capacity) by increasing uh. Note that $c = 0$ indicates depletion of the resource. Depleted resources cannot recover, so that ongoing migration into this environment cannot restore the resource. This also becomes apparent in $s(0, d_r) = 0$. Recall that the absence of capacity regulation amounts to $u(c, d_{rs}) = c$ for all d_{rs}, which is realized for $ub = uh = 0$.

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Compliance with ethical standards: Research for this theoretical study did not involve biological organisms.

Data availability: No empirical data was used, all parameters for the scenarios are listed in the text.