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1 **Hutchinson revisited: Patterns of density regulation and the**
2 **coexistence of strong competitors**

3

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1 **Abstract**

2 Ecologists have long been searching for mechanisms of species coexistence, particularly
3 since G.E. Hutchinson raised the ‘paradox of the plankton’. A promising approach to
4 solve this paradox and to explain the coexistence of many species with strong niche
5 overlap is to consider over-compensatory density regulation with its ability to generate
6 endogenous population fluctuations.

7 Previous work has analyzed the role of over-compensation in coexistence based
8 on analytical approaches. Using a spatially explicit time-discrete simulation model, we
9 systematically explore the dynamics and conditions for coexistence of two species. We
10 go beyond the analytically accessible range of models by studying the whole range of
11 density regulation from under- to very strong over-compensation and consider the
12 impact of spatial structure and temporal disturbances. In particular, we investigate how
13 coexistence can emerge in different types of population growth models.

14 We show that two strong competitors are able to coexist if at least one species
15 exhibits over-compensation. Analyzing the time series of population dynamics reveals
16 how the differential responses to density fluctuations of the two competitors lead to
17 coexistence: The over-compensator generates density fluctuations but is the inferior
18 competitor at strong amplitudes of those fluctuations; the competitor therefore becomes
19 frequent and dampens the over-compensator’s amplitudes, but it becomes inferior under
20 dampened fluctuations.

21 These species interactions cause a dynamic alternation of community states with
22 long-term persistence of both species. We show that a variety of population growth
23 models is able to reproduce this coexistence although the particular parameter ranges
24 differ among the models. Spatial structure influences the probability of coexistence but

1 coexistence is maintained for a broad range of dispersal parameters.

2 The flexibility and robustness of coexistence through over-compensation
3 emphasize the importance of non-linear density dependence for species interactions, and
4 they also highlight the potential of applying more flexible models than the classical
5 Lotka-Volterra equations in community ecology.

6

7 **Keywords:** Over-compensation, under-compensation, relative nonlinearity, Lotka-
8 Volterra, complex dynamics

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1 **1. Introduction**

2 The search for mechanisms of species coexistence has a long tradition in ecology.
3 Already Lotka (1925) and Volterra (1926) investigated this question with a theoretical
4 competition model in the early 20th century and found that intraspecific competition
5 must be greater than interspecific competition to facilitate coexistence of two species.
6 Gause (1934) complemented this finding by experimental work on *Paramecium* species
7 and concluded that two species competing for the same resources cannot stably coexist.
8 Hutchinson answered by raising the ‘paradox of the plankton’ (Hutchinson 1961). He
9 pointed to the apparent contradiction between the principle of ‘competitive exclusion’
10 (Gause 1934) and the existence of many highly diverse natural communities living on
11 strongly limited numbers of resources. This contradiction brings up the question which
12 mechanisms enable the number of coexisting species to exceed the number of available
13 resources (Armstrong and McGehee 1976; Lundberg et al. 2000; Szabo and Meszena
14 2006).

15 Coexistence mechanisms can be classified into equalizing and stabilizing
16 mechanisms (Chesson 2000). Equalizing mechanisms build on minimizing differences
17 in average fitness while stabilizing mechanisms rely on increased intra- compared to
18 interspecific competition strength, which disproportionately reduces the average fitness
19 of the more abundant species (Chesson 1994; Chesson 2000). Among the stabilizing
20 coexistence mechanisms, some depend on heterogeneous distributions of species in
21 space (i.e. spatial storage effects, Shmida and Ellner 1984; Hanski and Woiwod 1993;
22 Chesson 2000; Neuhauser and Pacala 1999). Others depend on fluctuations of
23 population densities in time and can foster coexistence via (1) temporal storage effects
24 or (2) different nonlinear responses to common fluctuating abiotic or biotic limiting

1 factors (Chesson 1994; Chesson 2003). In this context, the term ‘biotic’ refers to
2 explicitly modelled resource dynamics while the term ‘abiotic’ refers to a constant
3 limiting factor.

4 Temporal storage effects are based on external variations of the environment
5 causing species’ density fluctuations, e.g. through seasonal variations in resource
6 growth or strong and frequent disturbances (Smith 1981; Grover 1990; Anderies and
7 Beisner 2000; Abrams 2004).

8 Fluctuations of abiotic resources can emerge from different nonlinear consumer
9 responses and lead to the coexistence of many species on a handful of resources in
10 continuous-time models (Huisman and Weissing 1999). At least three resources are
11 needed, and there is an ongoing debate regarding the parameter space under which this
12 behaviour can be observed (Armstrong and McGehee 1976; Armstrong and McGehee
13 1980; Schippers et al. 2001; Huisman et al. 2001). In contrast, competition for biotic
14 resources can lead to the coexistence of two or more consumers on a single resource
15 (Armstrong and McGehee 1980; Zicarelli 1975; Abrams 2004; Kaitala et al. 1999). In
16 this case, coexistence requires at least two differences in species traits: first in the type
17 of functional response in resource use, and second in the minimum resource
18 requirements.

19 It is well known that fluctuations in population densities can also occur through
20 over-compensatory density regulation (May 1975; May 1976; Johst et al. 2008). In this
21 case, individuals scramble for coveted resources and populations over-compensate
22 deviations from carrying capacities which results in frequent peaks and crashes in
23 abundances (cyclic and chaotic dynamics). With compensatory density regulation,
24 individuals follow strategies that effectively avoid resource over-use and population

1 sizes fluctuate around the carrying capacity only due to stochastic events (equilibrium
2 dynamics). With under-compensatory density regulation, populations under-compensate
3 deviations from carrying capacities and the adjustment of population sizes to carrying
4 capacities is slow (delayed dynamics). For example, storage capacities may lead to a
5 delayed response if resources decline.

6 Over-compensatory density regulation and the resulting non-linear dynamics and
7 fluctuations have been investigated extensively with respect to single species
8 persistence (e.g., Ripa and Lundberg 2000; Murrell et al. 2002; Münkemüller and Johst
9 2006; Münkemüller and Johst 2007). However, few studies explored their contribution
10 to species coexistence. Damgaard (2004) expanded the Lotka-Volterra model of
11 coexistence (Volterra 1926; Lotka 1925) to a situation where both species exhibited the
12 same over-compensatory density regulation and showed that – in agreement with the
13 classical Lotka-Volterra competition model – coexistence was dependent on stronger
14 intraspecific than interspecific competition (i.e. only partial niche overlap). Other
15 authors found that differences in the types of density regulation can facilitate
16 coexistence under certain assumptions of landscape configuration and interaction
17 behaviour (Getz 1996; Johansson and Sumpter 2003; Edmunds et al. 2003; Kuang and
18 Chesson 2008). Analytically analyzing coexistence conditions at the limit of periodic
19 behaviour, Adler (1990) and Cushing (2007) provided evidence of oscillatory
20 coexistence of two species with complete niche overlap, i.e. intraspecific competition
21 equalling interspecific competition.

22 However, to date no study has systematically explored the robustness of
23 coexistence through over-compensation for a wide variety of density regulation types
24 (beyond the cyclic range including chaotic dynamics) and in a context that examines the

1 role of temporal disturbances and spatial habitat fragmentation. Here, we investigate
2 how different population growth models are able to display this coexistence.

3 We conduct these investigations using a time-discrete simulation model of
4 population growth. In a first step, we study community dynamics and analyse the
5 species-specific time series to better understand when and how two strong competitors
6 are able to coexist through over-compensatory density regulation. In a second step, we
7 investigate the impact of demographic parameters such as growth rate and carrying
8 capacity in four different population growth models. Finally, we investigate whether
9 space matters and how species' dispersal abilities (emigration rate and dispersal
10 mortality) influence coexistence through over-compensation.

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1 2. Model description

2 We simulate a two-species community with time-discrete dynamics. The species can
 3 differ in their density regulation type, but all other attributes are identical. Niches of the
 4 species can overlap completely, only partly, or not at all. The species live either in a
 5 homogeneous landscape or in a fragmented landscape with four patches connected via
 6 dispersal.

7 Time-discrete local population dynamics of the species A and B are described by
 8 an extended version of the Maynard Smith and Slatkin equation (MSS model) unless
 9 noted otherwise (1973; see also Hassell and Comins 1976):

10

$$N_A(t+1) \sim Pois \left(\frac{N_A(t) \cdot R}{\left(1 + (R-1) \left(\frac{N_A(t) + aN_B(t)}{K} \right)^{b_A} \right)} \right)$$

11

$$N_B(t+1) \sim Pois \left(\frac{N_B(t) \cdot R}{\left(1 + (R-1) \left(\frac{N_B(t) + aN_A(t)}{K} \right)^{b_B} \right)} \right)$$

12

13 The population sizes of species A and B at time t are given by $N_A(t)$ and $N_B(t)$. Both
 14 species have the same maximum growth rate, R , and common local carrying capacity K .

15 The competition coefficient a describes the strength of interspecific relative to
 16 intraspecific competition, to which we refer using the term ‘niche overlap’. It can be
 17 derived from the overlap of resource utilization curves along a resource axis (cf.
 18 Abrams et al. 2008). For most simulations we keep inter- and intraspecific competition
 19 strength equal (competition coefficient $a = 1$). Exceptions are the analyses without

1 interspecific competition ($a = 0$; Fig. 2) and those where we explore the effect of the
 2 competition coefficient on coexistence (systematic variation of a ; cf. Fig. 5). Both
 3 species differ only in their type of density regulation, which is characterized by b_A and
 4 b_B ($b < 1$ corresponds to under-compensating, $b = 1$ to compensating, and $b > 1$ to over-
 5 compensating density regulation). In this way, a wide range of combinations of density
 6 regulation types from under-compensation to strong over-compensation can be studied
 7 at given growth rates, carrying capacities and competition coefficients. We account for
 8 demographic stochasticity by using random numbers from a Poisson distribution. We
 9 independently and randomly initialize populations for each species by drawing from a
 10 uniform distribution between 10 and $10+K$ individuals.

11 For the comparative analysis we implemented further growth models. To
 12 simplify matters, we write them in a similar way with N_{all} referring to the weighted sum
 13 of individuals of both species (with weighting factor a , see MSS model for
 14 comparison): Similar to the MSS model, dynamics can be varied from equilibrium to
 15 cyclic and chaotic dynamics independently of R simply by increasing the value of
 16 parameter b (viz., type of density regulation).

17 Hassell model:
$$N(t+1) = \frac{R \cdot N(t)}{\left(1 + (R^{1/b} - 1)N_{all}(t)/K\right)^b}$$

18 Generalized Ricker model:
$$N(t+1) = N(t) \cdot e^{\ln R \cdot \left(1 - \left(\frac{N_{all}}{K}\right)^b\right)}$$

19 Gompertz type model:
$$N(t+1) = N(t) \cdot e^{\ln R \cdot \left(1 - \left(\frac{\ln N_{all}}{\ln K}\right)^b\right)}$$

20 In the fragmented landscape with four patches, dispersal occurs after local
 21 population growth. The population size after dispersal $N_i(t, d=1)$ is equal to the one prior
 22 to dispersal, $N_i(t, d=0)$, minus the number of emigrants, $N_{emi,i}(t)$, and plus the number of

1 immigrants. The number of emigrants per patch is drawn from a binomial distribution
 2 with $N_i(t, d=0)$ number of trials and emigration rate p_{emi} . The number of immigrants
 3 from patch i to patch j is drawn from a multinomial distribution with $N_{emi,i}(t)$ trials and
 4 transfer probability p_{ij} . The matrix of transfer probabilities, with entries p_{ij} , describes the
 5 probability to move from patch i to patch j . Values decrease exponentially with the
 6 Euclidean distance between patches, D_{ij} , measured in units of grid cells:

$$8 \quad p_{ij} = \frac{\exp\left(-\frac{1}{DD}D_{ij}\right)}{\sum_j \exp\left(-\frac{1}{DD}D_{ij}\right)} \cdot \exp(-mD_{ij})$$

9
 10 The mean distance over which both species are able to disperse is defined by DD , and
 11 the dispersal mortality rates are defined by m . The denominator scales the transfer
 12 probabilities p_{ij} such that they add up to one over all j in the absence of dispersal
 13 mortality (i.e. for the special case $m=0$). Emigration probability, dispersal distance and
 14 dispersal mortality rate m are equal for both species.

15 Temporal disturbances are introduced by an additional mortality rate; they occur
 16 after population growth and dispersal. Disturbances randomly reduce local density by
 17 $D_s(t) \cdot N(t)$ individuals, where $D_s(t)$ ranges from 0 to $D_{s,max}$ for each species and is
 18 independently drawn in each time step.

19

20 ***Simulation experiments and output***

21 We simulated population dynamics using reference values for the parameters if
 22 not noted otherwise (cf. Tab. 1). Reproduction rates were set to 5 per time step, which

1 seems reasonable for many species with low to medium body mass, e.g. for insects and
2 small mammals (Sinclair 1989). Local species' carrying capacity was 320 individuals.

3 In the time series analyses of species' densities (Figs. 1-3), we defined long-term
4 growth trends by estimating locally weighted linear fits for population sizes as a
5 function of time using a loess smoother (function `loess` in R 2.2.0, R Development Core
6 Team 2005). We measured the amplitudes of the over-compensating species' density
7 fluctuations via the absolute differences in the densities between consecutive time steps.
8 Again using a loess smoother for a locally weighted fit, we then analyzed how the
9 growth trends depend on amplitudes.

10 To investigate the role of niche overlap we varied the competition coefficient a
11 from 0 (no niche overlap) across 1 (complete overlap) to 1.2 (interspecific competition
12 stronger than intraspecific competition, cf. Fig. 4).

13 For the further and more extensive simulation experiments on the influence of
14 the growth model and space on coexistence (cf. Figs. 5, 6), we varied density regulation
15 from under-compensatory (minimum: $\ln(b) = -2$) to strong over-compensatory density
16 regulation (maximum: $\ln(b) = 2$) for both species. For each combination of density
17 regulation types, 100 simulations each with 1000 time steps were conducted, and from
18 these we derived the survival probability of each species as well as the coexistence
19 probability (proportion of simulations where both species survived 1000 time steps). To
20 validate coexistence probabilities we additionally analyzed invasibility and monitored
21 the probability to invade the population of the respective competitor with very few
22 invaders. Both analyses gave comparable results, and thus we only report coexistence
23 probabilities. We further repeated the experiments under the exclusion of demographic
24 stochasticity. We found no qualitative changes in the results and thus report only those

1 including stochasticity.

2 The simulation models were implemented with the Borland C++ Builder 5 using
3 numerical routines from the GNU Scientific Library (GSL Team 1992) for the
4 probability distributions. Graphics and statistics were generated in R 2.2.0 (R
5 Development Core Team 2005).

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1 3. Results

2 The simulations regarding coexistence of two species with equal competition coef-
3 ficients ($a = 1$, i.e. conspecific individuals cause the same competitive pressure as
4 heterospecific individuals) showed that competitive interactions of two identical
5 compensators ($\ln(b) = 0$) resulted in the random extinction of one species (Fig. 1a). The
6 same was true for two identical over-compensators. However, when a compensating
7 ($\ln(b) = 0$) and an over-compensating species ($\ln(b) = 1.5$) competed with each other,
8 both species were able to coexist (Fig. 1b, c).

9 Interspecific interactions dampened the fluctuations of the over-compensator, i.e.
10 amplitudes were much larger without interspecific interactions ($a = 0$, Fig. 2a) than with
11 interactions ($a = 1$, Fig. 1b, c). More specifically, amplitudes were buffered most
12 strongly when the compensating species was more frequent than the over-compensating
13 species. In contrast, amplitudes of the compensator were comparably strong without
14 ($a = 0$, Fig. 2b) and with interspecific interactions ($a = 1$, Fig. 1). The local regression
15 analysis between the over-compensator's amplitudes and species' growth trends
16 revealed two alternating and mutually advantageous dynamic situations for the species
17 (Fig. 3): (1) low to moderate amplitudes of the fluctuations resulted on average in a
18 positive growth trend of the over-compensator but in a negative growth trend of the
19 compensator; (2) for strong amplitudes, the situation was vice versa. This was found to
20 be a general pattern, but the absolute magnitude of the amplitude where the switch from
21 positive to negative growth rates for the over-compensator and the competitor occurred
22 (i.e., where both species displayed zero growth) varied between simulations. However,
23 within each simulation the switch point of zero growth was identical for both the over-
24 compensator and the competitor.

1 In addition to the experiments where intraspecific was equal to interspecific
2 competition strength ($a = 1$) and those without interspecific interactions ($a = 0$), we
3 gradually increased the competition coefficient a (Fig. 4). Species with equal density
4 regulation types (i.e., equal b) were able to coexist only if interspecific competition was
5 weaker than intraspecific competition ($a < 1$, Fig. 4a, left side of vertical line). How
6 weak it had to be depended on the type of density regulation. However, if species
7 differed in density regulation types and one species showed over-compensation,
8 coexistence was possible even if interspecific was equal to or stronger than intraspecific
9 competition ($1 < a < 1.2$, Fig. 4b, right side of vertical line). In particular, interspecific
10 competition allowed a strong over-compensator that could not persist in isolation to
11 coexist with another species (Fig. 4b, extinction of a strong over-compensator at
12 $a < 0.35$, but survival and coexistence with an under-compensator at $0.35 < a < 1.2$).
13 Hence, interspecific competition clearly broadened the survival range that resulted from
14 the various density regulation types.

15 In a next step, we conducted a comparative analysis for a range of demographic
16 parameters and growth models (Fig. 5) and analysed for which combinations of density
17 regulation types coexistence was possible. This consistently occurred when at least one
18 species showed over-compensation and the other species differed in its density
19 regulation type (Fig. 5, green area). No coexistence occurred when both species had the
20 same density regulation type (cf. cells along the diagonals). From under-compensation
21 to moderate over-compensation, the species with stronger over-compensation was
22 superior, i.e. species A outcompeted species B (Fig. 5, yellow areas), but from moderate
23 to strong over-compensation the species with less over-compensation was superior, i.e.
24 species B outcompeted species A (Fig. 5, blue areas). Increasing the carrying capacity

1 generally increased the number of density regulation types that were able to coexist with
2 each other. For small carrying capacities coexistence was either reduced to very small
3 ranges or was not possible at all (cf. plots for $K = 200$ vs. $K = 1000$).

4 The magnitude of the influence of growth rate depended on the growth model
5 that was chosen. While for the Ricker model coexistence was possible at small
6 reproduction rates (cf. plots with $R = 2$) and decreased at high reproduction rates
7 ($R = 20$), it was vice versa for the Hassell and the Gompertz type models. The MSS
8 model output was very robust to the choice of reproduction rate. Generally, at low
9 reproduction rates coexistence shifted to higher b values. Too low carrying capacities
10 did not allow for coexistence in any model.

11 In a final comparison, we evaluated the role of space for coexistence (cf. Fig. 6).
12 We used growth rates that led to robust coexistence in homogeneous space ($R = 2$ for
13 the Ricker model and $R = 20$ for all other models). Global carrying capacity was set to
14 500 (resulting in local carrying capacities of 125 individuals in the four patches).
15 Generally, fragmenting the available carrying capacity led to decreased coexistence.
16 However, coexistence was still much more probable than could be expected in a
17 completely isolated patch with a carrying capacity of 125 individuals. We further found
18 that increasing emigration rates resulted in decreased coexistence range (cf. plots with
19 $P_{emi} = 0.05$ vs. $P_{emi} = 0.4$). Including dispersal mortality slightly increased the
20 coexistence range through over-compensation. Additionally, a new coexistence
21 mechanism emerged: equal or very similar species (along the negative diagonal) were
22 able to 'neutrally' coexist, a mechanism well known from the literature (cf. Chesson
23 1994; Chesson 2000; Adler 2007). Qualitatively, results did not vary between different
24 growth models with the exception that coexistence was more robust to high emigration

1 rates for the MSS and Gompertz type models than for the Ricker and Hassell models.

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1 **4. Discussion**

2 Using a time-discrete population model we show that two strong competitors
3 (identical in their growth rates, carrying capacities and competition coefficients) are
4 able to coexist if (1) they differ in their types of density regulation and (2) at least one
5 species shows over-compensating density regulation. We found that this coexistence
6 occurs over a wide parameter range of density regulation types and proved robust to
7 model choice, temporal disturbances and spatial structure.

8

9 *4.1 Nonlinear population growth maintains coexistence*

10 Our analysis reveals the underlying dynamic mechanism (Fig. 3): The resulting
11 community dynamics are characterised by two dynamically alternating and mutually
12 advantageous biotic system states. These states are generated internally, and the
13 different fluctuation strength of the over-compensator's population density in these
14 states is the key element. At low to moderate fluctuations, the over-compensator is the
15 stronger competitor with a higher effective growth trend compared to the competitor
16 (Johansson and Sumpter 2003). This leads to increasing dominance of the over-
17 compensator's density in the population. However, high densities amplify the over-
18 compensator's intrinsic fluctuations. At strong fluctuations, the competing species can
19 use the emerging density depressions as temporal niches, provided that its density
20 regulation is more compensatory. Consequently, the competing species has the higher
21 effective net growth rate and increases its relative frequency in the population.
22 However, the over-compensator's fluctuations are buffered at a high frequency of the
23 competing species, and thus the over-compensator becomes the stronger competitor
24 again. In sum, coexistence through over-compensation is possible because the over-

1 compensator tends to generate fluctuations from which it suffers and the competing
2 species tends to dampen these fluctuations from which it benefits (Figs. 1, 3). These
3 alternating system stages can maintain coexistence both for competition coefficients
4 (i.e. degrees of niche overlap) that would lead to competitive exclusion in the classical
5 Lotka-Volterra equations (with linear density dependence; Fig. 4) and for strong over-
6 compensators that could not survive on their own due to strong endogenous fluctuations
7 and resulting deterministic extinction in the absence of a buffer (Fig. 4b).

8 Our simulation experiments show that various models that are well-established
9 in theoretical population ecology (e.g., Maynard Smith and Slatkin, Hassell, Gompertz,
10 Ricker) can display fluctuating coexistence through over-compensatory dynamics
11 similar to the oscillating coexistence in the more complex consumer-resource models
12 where the dynamics of consumers and resources are coupled explicitly (e.g., Armstrong
13 and McGehee 1980, Huisman and Weissing 2001, Abrams and Holt 2002, Wilson and
14 Abrams 2005). As coexistence through over-compensation results from differences in
15 the shape parameter b of the growth function, it can be associated easily with Chesson's
16 category of relative nonlinearity (Chesson 1994; Chesson 2000). Also, Kuang and
17 Chesson (2008) suggested a similar interplay between two alternating states for a plant
18 community facing seed predation. In their model the relative nonlinearity of the growth
19 functions was generated by life history trade-offs between seed productivity and
20 persistence in the seed bank rather than through density regulation. These different
21 studies highlight that considering not only the size of competition coefficients but also
22 the nonlinearity of population growth promises new insights into coexistence dynamics.

23

24 *4.2 Robustness of coexistence*

1 Our sensitivity analysis demonstrates that coexistence through over-compensation is
2 a feature of all four growth models, albeit for slightly different parameter ranges. As
3 endogenous density fluctuations result from the combined action of population growth
4 rate R , density regulation type b and the particular functional form of the population
5 growth model, different models lead to different coexistence ranges (Fig. 5). This
6 explains for example why the Ricker model exhibits coexistence at smaller R than the
7 Hassel model, or why the Gompertz model needs larger R than the MSS model to
8 maintain coexistence. Furthermore, our results show that only relatively large carrying
9 capacities can support coexistence through over-compensation. This is because large
10 mean population sizes buffer density fluctuations and help to prevent extinction during
11 density drops. Thus, our results suggest that communities relying on this coexistence
12 mechanism are likely to be sensitive to landscape fragmentation, in particular if
13 remaining patches are small. Yet, it is not high connectivity between patches (i.e., when
14 species have high emigration rates and low dispersal mortalities) that buffers the
15 fragmentation effect best, but low connectivity (low emigration rates, Fig. 6). The
16 reason is that coexistence through over-compensation depends on interacting and
17 alternating dynamics of the two species (as explained above). Too much exchange of
18 individuals between patches disturbs these dynamics and reduces coexistence. Thus,
19 limited dispersal is advantageous because it leaves local dynamics almost undisturbed
20 while still allowing for recolonization of extinct small patches, which supports
21 coexistence. This is quite different from coexistence through limited-dispersal
22 specialization where individuals disperse locally, either to exploit empty patches
23 quickly or to more rapidly increase densities in neighbouring patches to exclude
24 competitors (e.g. Bolker and Pacala 1999). Coexistence through over-compensation in

1 fragmented landscapes is a good example for a situation where a weak stabilizing
2 mechanism (coexistence through over-compensation cannot develop its full power due
3 to the small patch sizes) is supported by limited dispersal and only the two mechanisms
4 together lead to long-term coexistence (Chesson 2000; Adler 2007).

6 4.3 Relevance for real ecosystems

7 What is the relevance of this coexistence mechanism for real ecosystems? The type
8 of density regulation is a species trait that is difficult to measure in field experiments
9 (Godfray et al. 1990; Morris 1990). Even for time series derived from simulation
10 models, it is difficult to estimate the type of density regulation without an *a priori*
11 knowledge of the processes included in the model. In spite of these difficulties, many
12 researchers agree that different types of density regulation may have a significant effect
13 on ecosystem dynamics and functioning (reviewed in Hastings *et al.* 1993). For
14 example, several studies have provided evidence of chaotic dynamics due to over-
15 compensatory density regulation, in experimental as well as ‘natural’ conditions
16 (Godfray et al. 1990; Hastings et al. 1993). Field studies suggest over-compensating
17 density regulation as a possible mechanism in the competition for resources especially
18 for species with density regulation in early life stages (Sinclair 1989; e.g. for butterflies
19 such as cinnabar moths *Tyria jacobaeae*, beetles such as southern pine beetle
20 *Dendroctonus frontalis*, Reeve *et al.* 1998, or small mammals such as *Arvicola*
21 *terrestris*, Aars *et al.* 2001, and *Microtus ochrogaster*, Getz *et al.* 2006). We suggest
22 that particularly in communities with high species diversity but no apparent
23 differentiation in physiological characteristics or resource requirements, species
24 coexistence may rely critically on the differentiation in the types of density regulation as

1 demonstrated in our theoretical investigations. Examples may be the high small
2 mammal and insect biodiversity in some parts of the tropical rainforest zone or marine
3 plankton communities

4
5 In conclusion, we were able to show that the essence of coexistence through
6 over-compensation is the alternation of different dynamic community states emerging
7 from interacting species of different density regulation types. Coexistence is maintained
8 for a wide range of combinations of density regulation types, and it is also robust with
9 respect to the introduction of temporal disturbances and spatial structure as well as to
10 the choice of the particular non-linear model. Nevertheless, interesting questions for
11 future research remain, e.g., how these mechanisms may work if more species and
12 resources were involved, or how it could evolve in communities.

13 Our results clearly suggest that theoretical community ecology should go beyond
14 the linear density dependence of Lotka-Volterra equations. For example, for a better
15 understanding of spatial coexistence mechanisms it may be helpful to consider the
16 relevance of nonlinear density dependence for both local processes and resulting
17 equations for mean densities (moment equations, cf. Bolker and Pacala 1999).
18 Moreover, field studies should examine more closely competition types within
19 communities when studying coexistence. As scramble competition may lead to over-
20 compensating density regulation, a more detailed analysis of scramble versus contest
21 competition may give further insights into the functioning of communities.

22
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13

- 1 Table 1: Overview of parameters that were varied across simulation experiments,
- 2 parameters that were kept constant across all simulation experiments (but some were
- 3 drawn from given distributions), and output variables.
- 4

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1 Figure 1: Population densities of two competing species over 300 time steps on one
2 patch (for higher detail only the first 300 of 1000 time steps are shown): (a) equal types
3 of density regulation without disturbances, (b) different types of density regulation
4 without disturbances and (c) different types of density regulation with disturbances.
5 Intraspecific competition is as strong as interspecific competition ($\alpha=1$).

6

7 Figure 2: Population densities of two non-interacting species over 300 time steps on one
8 patch (for better detail only the first 300 of 1000 time steps are shown): (a)
9 compensating density regulation and (b) over-compensating density regulation.

10

11 Figure 3: Long-term trends in population growth of both species depend on the over-
12 compensator's fluctuation amplitudes. The figure provides an example for competing
13 species on one patch with disturbances (cf. Fig. 1c, Fig. 4b). The vertical line marks the
14 switch at which the growth trends of both species change their algebraic sign.

15

16 Figure 4: Coexistence probability of two species over 1000 time steps for different
17 competition coefficients and different density regulation types (uc: under-compensation,
18 $\ln(b)=-1$, c: compensation; $\ln(b)=0$, moc: moderate over-compensation, $\ln(b)=1.5$, and
19 soc: strong over-compensation, $\ln(b)=2$). In (a) the competing species have equal types
20 of density regulation and in (b) types of density regulation differ. The figures provide an
21 example for competing species on one patch with disturbances (cf. Fig. 1c, Fig. 3b). The
22 vertical lines mark the value of a where intraspecific equals interspecific competition
23 strength.

24

1 Figure 5: Coexistence of two species (green) in a homogeneous landscape. Species
2 differ only in their types of density regulation ($\ln(b)<0$: under-compensation, $\ln(b)=0$:
3 compensation, $\ln(b)>0$: over-compensation). We compared different population growth
4 models (in the columns: Maynard Smith and Slatkin, Hassell, Ricker, Gompertz type) at
5 different values for reproduction rates ($R=2$ or 20) and carrying capacities ($K=200$, 500
6 or 1000). The colours code the competition outcome: green marks coexistence
7 probability ≥ 0.2 , yellow marks coexistence probability < 0.2 and persistence
8 probability of species A ≥ 0.5 , blue marks coexistence probability < 0.2 and persistence
9 probability of species B ≥ 0.5 , and grey marks simulations where none of the conditions
10 is fulfilled. The presented output for $b_A \geq b_B$ is equal to the output of $b_A \leq b_B$ because
11 species only differ in b (white marks not simulated parameter combinations).

12
13 Figure 6: Coexistence of two species (green) in a fragmented landscape with four
14 patches. Species differ only in their types of density regulation ($\ln(b)<0$: under-
15 compensation, $\ln(b)=0$: compensation, $\ln(b)>0$: over-compensation). We compared
16 different population growth models (in the columns: Maynard Smith and Slatkin,
17 Hassell, Ricker, Gompertz type) at different values for dispersal mortality ($m=0$ or 0.2)
18 and emigration rates ($P_{emi}=0.05$, 0.1 or 0.4). The colours code is the same as in Fig. 5.

1

Parameters that varied across simulation experiments			
<i>Symbol</i>	<i>Parameter</i>	<i>Reference</i>	<i>Experiments</i>
R	Reproduction rate	5	[2;20]
a	Competition coefficient	1	[0;1.2]
K	Local carrying capacities	320	[125;1000]
b_A, b_B	Type of density dependence	$[e^{-2}; e^{2.4}]$	$[e^{-2}; e^2]$
m	Dispersal mortality rate	-	0 or 0.2
P_{emi}	Emigration rate	-	[0;0.4]
P_{Number}	Patch number	1	1 or 4
$D_{s,max}$	Max. disturbance mortality	0.05	0 or 0.05
Parameters that were kept constant across all simulation experiments			
<i>Symbol</i>	<i>Parameter</i>	<i>Values</i>	
	Initial population size per species	10	
L_{Size}	Lattice size [cells ²]	20*20	
DD	Mean dispersal distance [cells]	1,2,6,12,20	
Output variables			
<i>Symbol</i>	<i>Variable</i>		
$N(t)$	Individual number over time		
	Survival probability		
	Coexistence probability		

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