Testing the intermediate disturbance hypothesis in species-poor systems: A simulation experiment for mangrove forests

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Abstract

Questions: What factors influence tree species diversity of mangrove forests, an example of species-poor systems? What are the respective importance and interactions of these factors? Is the intermediate disturbance hypothesis applicable to such systems?

Methods: We used the spatially explicit individual-based model KiWi to investigate the effects on species diversity of perturbation frequency and intensity, different abiotic conditions, and interspecific competition simulated at the individual level. The simulation system considered the three dominant Caribbean mangrove species: *Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa*, applying species-specific growth and mortality characteristics. Firstly, effects on species dominance of the abiotic conditions nutrient availability and porewater salinity were tested with two competition scenarios. Secondly, the effect of perturbation frequency and intensity were investigated with selected abiotic conditions.

Results: Abiotic conditions influenced species dominance and, in extreme cases, excluded one or two species. Abiotic and competition settings controlled the successional dynamics and the response of species dominance to perturbation regimes. A response consistent with the intermediate disturbance hypothesis was observed only with a configuration of plant interaction in which one species behaved as a pioneer so that succession occurred by competitive exclusion.

Conclusions: We suggest that successional dynamics interact with the intensity and timing of perturbations and determine whether or not mangrove tree diversity conforms to predictions of the intermediate disturbance hypothesis. For mangroves, these successional dynamics are site-specific depending on abiotic conditions and species configurations.

Keywords: Individual-based modeling; Interspecific competition; KiWi model; Perturbation regime; Species dominance; Succession.

Abbreviations: FON = Field of Neighbourhood; IDH = Intermediate disturbance hypothesis; I_{SDH} = Index of species dominance heterogeneity; psu = Practical salinity units; RNA = Relative nutrient availability.

Introduction

For several decades, plant ecologists have tried to understand the processes implicated in variations in species diversity (e.g. Chust et al. 2006 see reviews by Loreau et al. 2001; Barot & Gignoux 2004; Vellend & Geber 2005). Among these processes, perturbations have been considered of high importance and have led to an ongoing debate on the intermediate disturbance hypothesis, which states that species richness is maximized at intermediate levels of disturbance (Grime 1973; Connell 1978; see reviews by Mackey & Currie 2001; Sheil & Burslem 2003; Shea et al. 2004). The situation of mangroves along tropical coastlines favours potential damage by major destruction events such as hurricanes or tropical storms (Imbert et al. 1998). Smith & Duke (1987) addressed the question of disturbance effects on mangrove tree diversity in Northern Australia. They showed that species richness decreased with increasing hurricane frequency. However, very few studies have analysed changes in mangrove species composition in relation to perturbation regime (Baldwin et al. 2001; Piou et al. 2006), and none have evaluated the implicated processes behind these effects. A straightforward explanation for this lack of consideration is the low number of tree species on mangrove systems. For example, in the Caribbean region, which is a hot spot of hurricane activity, only three to four true mangrove species are found. Thus, studies on tree species diversity are mostly seen as superfluous in this system.

However, considering species diversity as an expression of species richness and evenness (Kempton 1979), systems with only three species could also vary in species diversity. Piou et al. (2006) used an adaptation of the Simpson's reciprocal index of species diversity (Simpson 1949; Hill 1973) to determine that the destruction intensity at different mangrove sites in Belize had an effect on the heterogeneity of species dominance. Although the patterns in Belize differed from other situations (e.g. Baldwin et al. 2001), it indicated

that the effects of large destruction on species diversity also exist for species-poor mangrove systems. Based on these findings, we chose to use the Caribbean mangrove system as an example for analysing factors and processes influencing species diversity in species-poor systems.

Our first hypothesis was that the succession of species dominance depends on both the interspecific competition configuration and the abiotic conditions. The second and more general hypothesis was that the resulting succession trajectories determine the type of response of the system to perturbations, and the eventual production of a bell-shape pattern of species diversity with intermediate perturbation regime. To test these hypotheses, we investigated the effects on species diversity of perturbation frequency, perturbation intensity, different abiotic conditions, and interspecific competition by means of simulation experiments with an individual-based model.

Methods

KiWi model: General settings

The experiments were carried out with the spatially explicit mangrove model KiWi (Berger & Hildenbrandt 2000, 2003), developed as dynamic library software written in C++ and using an interface in Microsoft ® Visual Basic ® (DLL and examples available from the corresponding author). The KiWi model describes resource competition on the level of individuals and simulated growth of mangrove stands composed of the three main Caribbean species, *Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa*. The gap model FORMAN (Chen & Twilley 1998) provided the growth formulas, multipliers for nutrient and salinity effects and respective parameters. It is important to note that the KiWi model is not a gap model since it describes trees individually and is spatially explicit. We used Berger & Hildenbrandt's (2000) innovation of the field of neighbourhood (*FON*) approach, which simulated inter-individual competition for space and resources. We assumed that the *FON* described the area where a tree influenced its neighbours and was influenced by them by sharing limiting resources such as light or nutrients. The *FON* was defined as a circular intensity field that decreased from the center (stem position) out to the boundary. It specified the intensity of competition exerted by a tree at any position within its neighbourhood.

The growth of each individual tree was calculated with the following formula (Berger & Hildenbrandt 2000):

$$\frac{\Delta DBH}{\Delta t} = \frac{G \times DBH \times \left(1 - \dfrac{DBH \times H}{DBH_{max} \times H_{max}}\right)}{274 + 3 \times b_2 \times DBH - 4 \times b_3 \times DBH^2} \times f_s(SALT) \times f_n(RNA) \times f_c(F_A) \quad (1)$$

where: *DBH* was the stem diameter at breast height (cm);

H was tree height (cm); DBH_{max} and H_{max} were maximum values of diameter and height for a given tree species; G, b_2 and b_3 were species-specific growth constants and the three f-functions were growth multipliers (see App. 1 for details or Chen & Twilley 1998). The growth multipliers $f_s(SALT)$ and $f_n(RNA)$ considered the effects of the porewater salinity and relative nutrient availability, respectively (Chen & Twilley 1998). The function $f_c(F_A)$ was the growth multiplier for the *FON* effect on growth (Berger & Hildenbrandt 2000):

$$f_c(F_A) = \max\{0 \; ; \; 1 - \varphi \times F_A\} = \max\left\{0 \; ; \; 1 - \varphi \times \left(\frac{1}{A}\sum_{n \neq k}\int_o FON_n(x,y)\,do\right)\right\} \quad (2)$$

where: φ was an arbitrary maximum value of effect of competition simulating resource sharing capacity, A was the *FON* area of the focus tree k, n were the neighbours of k, belonging to the focal and neighbour tree n, and the FON_n function was the intensity of competition of the neighbour n at each point of O. The *FON* function was calculated as:

$$FON_n(r) = \begin{cases} 1 & for \; 0 \leq r < RBH \\ \exp\left(-\left(\dfrac{|\ln(F_{min})|}{R - RBH}\right) \times (r - RBH)\right) & for \; RBH \leq r \leq R \\ 0 & for \; R < r \end{cases} \quad (3)$$

where: RBH was the radius of the stem at breast height of n, r was a distance from the stem position of n, and F_{min} was the minimum intensity of the *FON* (0.1, Berger & Hildenbrandt 2000) at the *FON* radius (R). This *FON* radius (R) depended on the size of the tree:

$$R = a \times RBH^b \quad (4)$$

where: a and b were scaling parameters (cf. 'setting interspecific competition' and App. 2). The value of b determined inversely the competition intensity of individuals (see Berger & Hildenbrandt 2003 for variations of model behavior depending on these two parameters).

According to the assumption of Chen & Twilley (1998), an overall availability of recruits was considered as RN_{tot} = 18 saplings.100m^{-2}.yr^{-1} (Chen & Twilley 1998). However, the annual number of recruits varied randomly, and the number from each species (RN_i) was proportionally set according to the occurrence of mature trees (height >5m) of each species:

$$RN_i = int\left(rnd_1 \times p_i \times RN_{tot} + rnd_2 \times RN_{tot}\right) \quad (5)$$

where: rnd_1 was a uniform random number between 0.5 and 1.5; rnd_2 a uniform random number between 0.1 and 0.3; and p_i the proportion of mature trees of species i over the total number of mature trees in the plot. The range of variation of rnd_1 was chosen to describe a natural fluctuation in the availability of recruits per species (+/-50%). The range of variation of the rnd_2 provided an occasional reappearance of an already excluded species. These two

ranges of variations were set arbitrarily, but a sensitivity analysis showed a low effect of these parameters on the main results (App. 3). The recruits were installed randomly on the simulation area, but were removed if the *FON* intensity (sum of $FON(x,y)$ of all trees at the point of installation x, y) was higher than the species-specific threshold (F_{Amax}). This threshold was set to $F_{Amax} = 0.5$ for *R. mangle* (Berger & Hildenbrandt 2000) and assumed as $F_{Amax} = 0.0$ for the two other species to simulate the shade intolerance of seedlings of *L. racemosa* and *A. germinans* (Ball 1980; McKee 1993). Mortality of individual trees not due to external perturbations was growth-rate dependent as described by Berger & Hildenbrandt (2000).

Settings of interspecific competition parameters

The growth parameters and effects of salinity and nutrient availability (DBH_{max}, H_{max}, G, b_2, b_3, f_s and f_n, Eq. A1.1, see App. 1) created species-specific differences in growth response at the stand level. For additional variation in interspecific competition, we considered two ways of simulating spatial competition at the individual level. The first considered an equal effect of neighbouring competition for trees of the same size for the three species. Thus, they had the same resource sharing tolerance ($\varphi = 2.000$, Berger & Hildenbrandt 2000) and identical a and b parameters (11.0, 0.64, respectively, cf. App. 2, Fig. A2.1). Since the interspecific competition in this parameterization was only through the relative growth rate of each species, it is hereafter referred to as *species homogeneous spatial competition*. The second parameterization considered that each species had spatially-specific competition strength. Particularly, *L. racemosa*, which was described as heliophilic (Wadsworth 1959; Ball 1980; Roth 1992) was set to have a lower sharing tolerance ($\varphi = 2.222$, assuming that the maximum F_A was 10% lower than the other species, i.e., maximum $F_A = 0.45$). Additionally, species-specific a and b parameters (App. 1, Table A1.1) were used to describe the canopy and root-system differences for the three species. These parameters were tuned (App. 2, Fig. A2.1) to reproduce field data of monospecific stands of tree size / density relationships from Belizean offshore mangroves, and to set *L. racemosa* as less competitive than the two other species. This lower competition capacity of *L. racemosa* was at DBH < 80 cm; while the a and b values also determined that *A. germinans* was more competitive than *R. mangle* at DBH > 20 cm. This second parameterization is hereafter referred to as *species heterogeneous spatial competition*.

Effects of abiotic conditions

Our first exercise was set to analyse the effect of abiotic conditions on species diversity without any perturbations. We also investigated the effect of interspecific competition on succession of species dominance in this exercise. Five salinities (0, 20, 40, 50 and 60 psu) and four relative nutrient availabilities (*RNA*) (100%, 80%, 60% and 40%) were considered. Ten replicates of all possible salinity/*RNA* scenarios on the two competition parameterizations were simulated on a 6000-m² plot and over 1000 years.

The number of trees and basal area per species were used to calculate relative abundance and dominance for each time step and transformed into importance values (*IV*) according to Cintrón & Schaeffer-Novelli (1984):

$$IV_i = \frac{100 \times Dens_i}{\sum\limits_{j=1}^{q} Dens_j} + \frac{100 \times BA_i}{\sum\limits_{j=1}^{q} BA_j} \qquad (6)$$

where: IV_i, BA_i and $Dens_i$ were the importance values, basal area and density of trees of the species i, and q was the number of species. As a measure of species diversity, we used the index of species dominance heterogeneity (I_{SDH}) from Piou et al. (2006). It was adapted from the reciprocal index of Simpson (Hill 1973) and computed as follows:

$$I_{SDH} = \frac{\sum\limits_{i=1}^{q} IV_i \times \left(\sum\limits_{i=1}^{q} IV_i - 1 \right)}{\sum\limits_{i=1}^{q} \left(IV_i \times (IV_i - 1) \right)} \qquad (7)$$

This index indicated relative species dominance in our three-species system and was given a value of 0 if no trees could grow because of harsh abiotic settings. If trees could grow, the I_{SDH} were given values from 1 (only one species present on the plot) to 3 (the three species representing each 33% of importance on the plot). Since this index was not mathematically independent from species richness, we decided not to use the term 'evenness' to avoid confusion with its calculations in community studies (Smith & Wilson 1996). However, through the variation of relative species dominance, this index could indicate if different three-species configurations of our system were relatively rich or not in term of species diversity. As indicators of salinity/ RNA effect on species diversity, the median, 1st. and 3rd. quartiles of I_{SDH} for each scenario over the last 400 yr of simulations were calculated.

Effects of perturbation regimes

The second exercise was set to analyse the effects of perturbation regimes on species diversity. Massive killing events, which simulated mortality induced by a tropical storm or hurricane, were applied at different mortality rates (intensity) and frequencies. Because there is inconsistency in the literature on the way authors described storm resistance capacity according to species or tree size (e.g. Vermeer 1963; Stoddart 1963; Bardsley 1984; Roth

1992, 1997; Smith et al. 1994; Imbert et al. 1998; Sherman & Fahey 2001; Baldwin et al. 2001; Imbert 2002), we could not consider the mortality events related to size or species in our simulations. The applied intensities were probabilities of 30%, 50%, 70%, 90% and 99% of mortality for each tree at the event times. The perturbation frequencies (1 /100 yr, 1 /80 yr, 1 /60 yr, 1 /40 yr, 1 /20 yr and 1 /10 yr) determined the exact number of years between two events.

To achieve a stabilized system in term of number of trees, we excluded the first 400 simulation years. Perturbations were applied only on the following 400 years so that the total simulated time was 800 years. The role of abiotic conditions on system response to perturbation was considered by selecting scenarios from the results of the previous exercise. Benign (salinity 0 psu and 100% RNA) and medium (salinity 50 psu and 80% RNA) conditions were analysed, but extreme ones were not considered because they resulted in a system overwhelmed by one species. Ten replicates were simulated for each abiotic scenario (benign or medium) for each competition parameterization (*homogeneous* or *heterogeneous spatial competition*) and all mortality rate/perturbation frequency scenarios. Similar to the previous exercise, the median of I_{SDH} was calculated over the last 400 yr for all cases. To analyse the significance of perturbation intensity with selected perturbation frequency, Kruskal-Wallis non-parametric analysis of variance (ANOVA) by ranks were applied on the last I_{SDH} values of each simulation. To analyse the effect of perturbation frequency with selected perturbation intensity, identical non-parametric ANOVAs were done considering all the I_{SDH} values of the simulated perturbation time. Mann-Whitney U tests were used to assess significant differences of extremes and intermediate I_{SDH} values in order to validate disturbance effect patterns such as U-shaped, linear increase or decrease, irregular or bell-shaped.

Results

First exercise: effects of abiotic conditions

Extremely low relative nutrient availabilities (40% RNA) and extremely high salinities (60 psu) decreased significantly the index of species dominance heterogeneity (I_{SDH}) for both spatial competition parameterizations (App. 4, Fig. A4.1). These extreme abiotic conditions caused species exclusion through the parameterization of *R. mangle* and *A. germinans* growth characteristics to be non-adapted to high salinities and low nutrient availabilities, respectively. At the worst condition (salinity 60 psu and 40% RNA), no species grew at all, resulting in $I_{SDH} = 0$. Considering the rest of the abiotic scenarios,
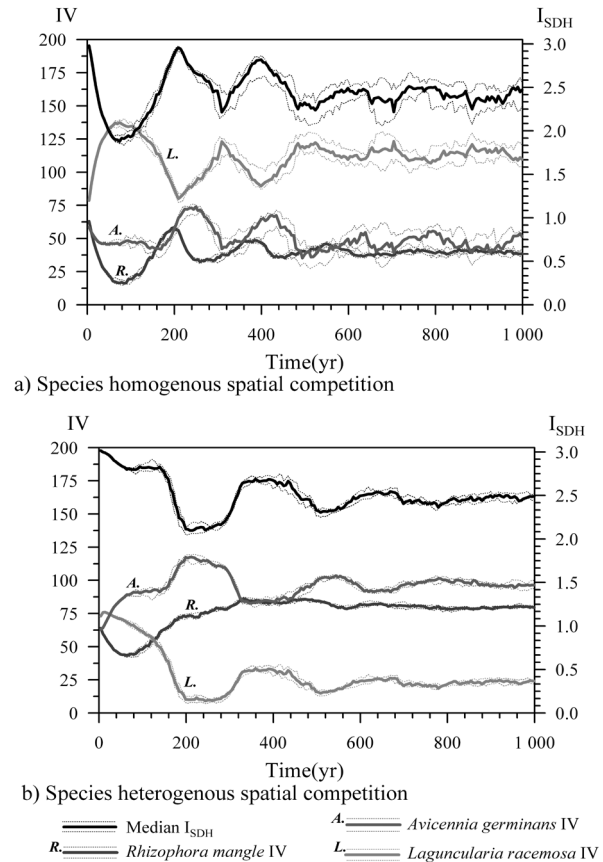

a) Species homogenous spatial competition

b) Species heterogenous spatial competition

Median I_{SDH} — *A.* *Avicennia germinans* IV
R. *Rhizophora mangle* IV — *L.* *Laguncularia racemosa* IV

Fig. 1. Dynamical variations of the two competition parameterizations with selected abiotic scenarios (medium = Salinity 50 psu and RNA 80%) in species relative importance (*IV*) and I_{SDH} (thin lines = respective first and third quartiles).

highest I_{SDH} values in both spatial competition parameterizations were found at intermediate levels of salinity and *RNA*. The median I_{SDH} values over the last 400 yr were relatively similar between the two spatial competition parameterizations. However, I_{SDH} and species importance values varied more importantly during the first 400 yr for all abiotic scenarios. For medium abiotic scenario (e.g., salinity 50 psu and 80% *RNA*), variations of species importance values showed a cycling of species dominance (Fig. 1). The *species heterogeneous spatial competition* parameterization created a quick succession from *L. racemosa* to *A. germinans* (Fig. 1b) during the first 50 yr of simulations. With *homogeneous spatial competition*, the dominance of *L. racemosa* varied but stayed always higher than the two other species (Fig. 1a). Identically, for benign abiotic scenarios, the *species heterogeneous spatial competition* created species succession, while the *homogeneous spatial competition* showed importance values variation without shift of species dominating.
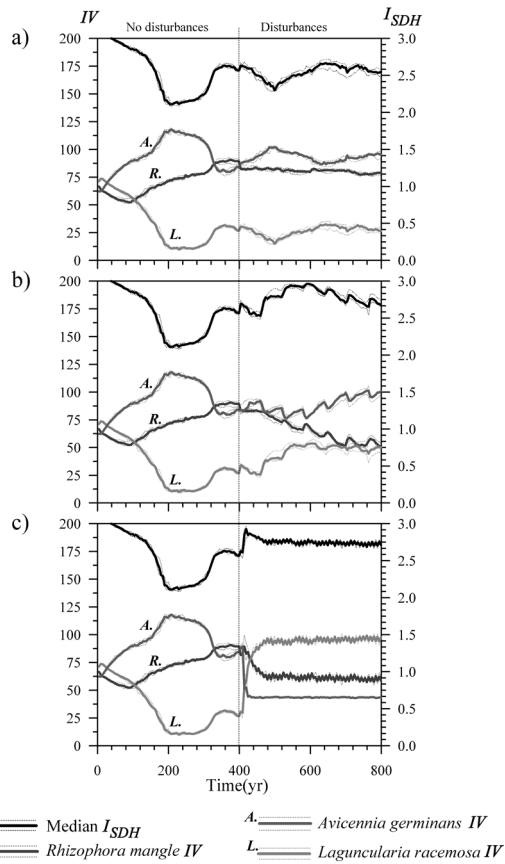
Fig. 2. Dynamical variations in species relative importance (*IV*) and I_{SDH} for the heterospecific competition parameterization and medium case of abiotic scenario (salinity 50psu, 80% RNA), for different perturbation regimes. **a.** frequency= 1 / 100 yr, intensity = 30% mortality; **b.** frequency = 1 / 60 yr, intensity = 70% mortality; **c.** frequency = 1 / 10 yr intensity = 99% mortality). (thin lines = respective first and third quartiles).

Second exercise: effects of perturbation regimes

For the analysis of phenomena explaining the response pattern, we concentrated only on the medium abiotic scenario. Massive mortality altered the temporal dynamic of I_{SDH} (Fig. 2). The low perturbation regime (Fig. 2a) did not modify the general trend of variation of species importance values and I_{SDH} compared to non-disturbed dynamics (Fig. 1b). With an intermediate perturbation regime (more frequent and stronger disturbances, Fig. 2b compared to 2a), *L. racemosa* gained in importance although still less important than the two other species. This reduced the difference in relative importance of the three species and thus led to an overall higher I_{SDH} than with the low perturbation regime. The most frequent and destructive perturbation regime (Fig. 2c) switched the system quickly from *A. germinans* to *L. racemosa* dominance. At this level of perturbation regime, each disturbance had an effect of
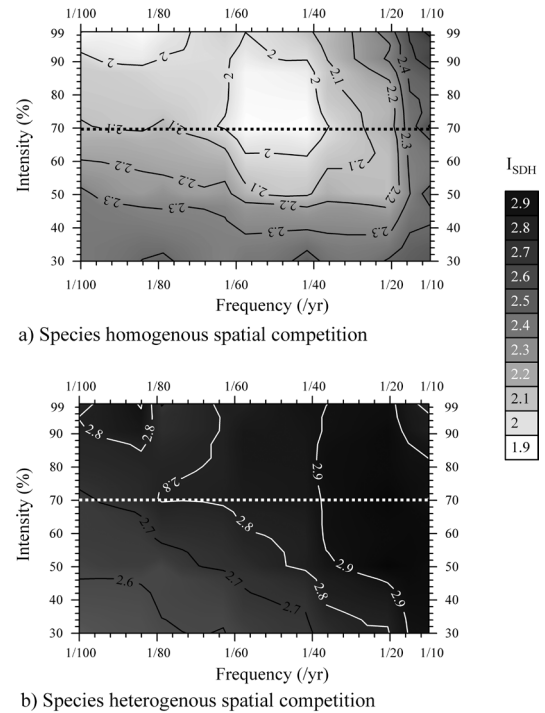

a) Species homogenous spatial competition

b) Species heterogenous spatial competition

Fig. 3. Median I_{SDH} variations according to perturbation frequency and intensity for the two competition parameterizations (**a** and **b**) with medium abiotic scenario (Salinity 50 psu and 80% RNA). Dashed lines represent selected pattern illustration for Fig. A4.2-2 (App. 4).

keeping *L. racemosa* as the most important species on the plot. This corresponds to the original succession situation at the beginning (first 10 years) of the simulations, as if *L. racemosa* were the pioneer species of the system. However, this change of dominance did not modify significantly the I_{SDH} values compared to low or absent perturbations because the ratios of species importance values were conserved. In this case, the high frequencies stabilized these ratios and I_{SDH} values over time.

Variations in perturbation regimes always had an effect on the species dominance heterogeneity of the simulated stands (Fig. 3). However, the overall patterns of simulation results depended on the different competition parameterization. The *species homogeneous spatial competition* parameterization (Fig. 3a) showed lower I_{SDH} values at intermediate perturbation regimes than at lower and higher perturbation frequencies and intensities. This U-shaped curve pattern was clearly observable as to the influence of frequency regime with a selected perturbation intensity (following line on Fig. 3a or App. 4, Fig. A4.2a), although the values showed high variation among simulations (1st. and 3rd. quartile variations). The *species heterogeneous spatial competition* parameterization resulted in an overall increase in I_{SDH} values with increasing disturbance regimes until non-extreme intensity and frequency followed then by a small decrease (Fig. 3b). Thus, this trend led to an

overall bell-shaped pattern, which was also more visible for the influence of frequency regime with selected perturbation intensity (following line on Fig. 3b or App. 4, Fig. A4.2b).

Analysing the patterns for all scenarios, we found a clear difference of patterns between the two spatial competition parameterizations. The *homogeneous spatial competition* parameterization led to some cases of U-shaped patterns while the *heterogeneous spatial competition* on the contrary showed bell-shaped patterns. However, not all perturbation regimes led to these U- or bell-shaped patterns, but also included cases of linear increasing or decreasing patterns or even non-significant or irregular patterns. These trends were repeated with the two selected abiotic conditions (cf. App. 4, Fig. A4.3 for detailed results).

Discussion

This study illustrated that even for species-poor systems, the dynamics and the processes that could explain variations in species diversity are diverse and interconnected. The interplay of abiotic conditions and interspecific competition produces a set of potential vegetation dynamics. Depending on the perturbation regime, a system will follow a particular trajectory of this set, and eventually test the expectations of the intermediate disturbance hypothesis pattern.

Our simulations integrate the actual knowledge on Caribbean mangrove species of species-specific parameterization of growth, adaptations to abiotic conditions, settlement, and spatial competitive strength. The results of the first exercise illustrate that abiotic conditions influence the dominance distribution of these species, up to eventually excluding one or more species. On the contrary, intermediate conditions of porewater salinity and nutrient availability favorable to all three species lead to higher coexistence. The setting of species-specific growth parameters of our model is thus able to re-create the diversity of species dominance observed in the Caribbean. Other factors that were not considered in this study, such as tidal regime, temperature, soil physico-chemical properties (e.g., redox potential or sulfide contents), could have similar effects on species richness and dominance in mangrove systems (Ball 1980; McKee 1993).

The results of the first exercise also show that changes in the characteristics of species-specific spatial competition do not modify significantly the overall measure of species diversity. However, at a given abiotic condition, a change in the settings for spatial competition drastically alters the temporal variations of relative species dominance. Our parameterization of *homogeneous spatial competition* leads to a cycling dynamic but with *L. racemosa* dominating all

the time because of its faster growth rate. The hypothesis behind this parameterization is that species differ in their resource use capacity but not in a spatially explicit way. For example, trees of the same size would have the same spatial extent of resource use disregarding their species. In contrast, the *heterogeneous spatial competition* parameterization is derived from the hypothesis that individuals of *L. racemosa* are less competitive for spatially distributed resources than individuals of other species (Wadsworth 1959; Ball 1980; Roth 1992). The reduction of resource-sharing tolerance for the *L. racemosa* trees increased the effects of neighbours on their growth rates. Additionally, species-specific changes in the FON radius influenced species interactions by conferring lower competitive strength to *L. racemosa* individuals than equal-sized *A. germinans* or *R. mangle* trees. Thus, after the first years of fast growth of *L. racemosa* trees this *heterogeneous spatial competition* parameterization produced a shift in dominance. Thus, this succession resulted from the switch in the importance of two forces: (a) the primary growth rate of *L. racemosa*, which is known to be faster than for the other species under low salinity conditions, high nutrient, and light availability (McKee 1995; Sherman et al. 1998; Lovelock & Feller 2003); and (b) the low strength of spatial interspecific competition of *L. racemosa* (as hypothesized by Berger et al. 2006). These characteristics are typical of pioneer-like species in any plant system. In mangrove forests, such successions were described in some secondary recovery areas (Ball 1980; Berger et al. 2006), which suggests that our second spatial competition parameterization is supported by field observations. These differences in the dynamics between the two parameterizations become especially important when considering the effects of perturbations.

The simulations with perturbations illustrated that species dominance of our system depended on the frequency of the destruction events and their intensities. However, we have seen that the pattern of response changed mainly depending on the competition parameterization and thereby the successional dynamic. Perturbations created gaps that would take the same trajectory as the system's dynamics observed without perturbations. For each gap recovery, the seedling availability depended on the dominant species in the rest of the stand. In the case of *homogeneous spatial competition* parameterization, if the system was perturbed each time when the majority of gaps were in the cycling phase of highest dominance of *L. racemosa*, the dominance of this species would increase more and more, as in a resonance phenomenon. This situation was created at intermediate perturbations regimes, leading to the lowest I_{SDH} values. With extreme disturbance regime, the system would achieve the cycling phases earlier and, thus, would return to a more even species distribution. This scenario led to higher I_{SDH} values, and overall created the observed U-shaped patterns. With the *heterogeneous spatial competition*

parameterization, perturbations caused the system to return reiteratively to conditions seen during the initial succession phases. Since *L. racemosa* was the most pioneer-like of the three species, it obtained higher importance with stronger and more frequent perturbations, which created a more homogeneous species dominance. Eventually, with extreme perturbation regimes, *L. racemosa* dominated completely, reducing the index of species dominance heterogeneity. In mangrove forests, it is therefore possible to observe the bell-shaped pattern typically described by the intermediate disturbance hypothesis (IDH) (Connell 1978) if we have a biotic configuration where *L. racemosa* is pioneer and succession happens during stand recovery or establishment. However, in addition to bell-shaped or U-shaped patterns, our results also revealed many cases of linear increases or decreases due to perturbation regimes not fitting exactly the resonance of the recovery dynamics.

This diversity of responses to perturbation fits the observations of Mackey & Currie (2001) and the prediction of the IDH axioms detailed by Sheil & Burslem (2003). Specifically, to have an IDH pattern one needs: (1) a dominance successional sequence when no perturbations occur; (2) succession due to competitive exclusion of fastest growing trees; and (3) perturbations that bring the system back to earlier successional stages. The results of our individual-based model simulating competition at individual-level confirm these axioms. The *homogeneous competition parameterization* of our study did not create succession and therefore did not exhibit a pattern predicted by the IDH. However, this dynamic is possible in nature (e.g. in understorey species systems as in Beckage & Stout 2000) and in mangrove ecosystems particularly. Only few studies have observed a real species succession in mangrove forests (e.g., Ball 1980; Berger et al. 2006). Lugo (1980) concluded that zonation was a steady state result of abiotic conditions and refuted Davis' (1940) hypothesis that zonation was the result of succession and land building processes. Since Lugo's paper, succession in mangroves has been cautiously attributed to changes in abiotic conditions because of external factors, but rarely to species-induced modifications of abiotic conditions (e.g., Bertrand 1999). Because the IDH pattern is the expression of the dynamics of species succession, it can be used to compare species succession at different disturbance levels, or conversely, to compare the recovery dynamics of sites that exhibit different succession dynamics. Both aspects have never been considered in mangrove ecology. Such studies could support our simulation results that in some cases succession could be due to plant-plant interactions and not always exclusively to changes in abiotic conditions.

Finally, our study at the individual level demonstrates that even if abiotic conditions strongly influence species composition in mangrove forests, spatial plant-plant interactions also play an important role. We showed that the successional dynamic is dependent on the capacities of individuals of different species to compete spatially for resources, and that these dynamics determine the way species diversity will increase or decrease in case of perturbations. Thus, we demonstrate that variations of mangrove species diversity due to perturbation regime will depend on a series of interacting factors, including succession configuration, actual dynamic phases, plant spatial interactions, and abiotic settings. Additionally, field studies show that changes of abiotic settings after perturbations (e.g., Cahoon et al. 2003), recruitment patterns (e.g. Baldwin et al. 2001; Clarke 2004; Piou et al. 2006) and also differences of resistance of species to the considered perturbations (Baldwin et al. 2001; Imbert 2002) could influence species composition of mangroves. Hence, forecasting a general trend of evolution of species diversity of mangrove forests only considering the perturbation regime seems risky. It could be possible only in a site-specific case, knowing not only the abiotic conditions of a particular site, but also the type of species interactions and succession phenomenon that could occur.

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For App. 1-4, see below (online version)
also available at JVS/AVS Electronic Archives;
www.opuluspress.se/

App. 1. Details on growth multipliers and parameters.

In this appendix, we give the details of the growth multipliers and parameters (Table A1.1) entering in Eq. A1.1. The function $f_s(SALT)$ was the growth multiplier considering the effect of the pore water salinity on growth (Chen & Twilley 1998):

$$f_s(SALT) = \frac{1}{1 + \exp(d \times (S_{0.5} - S))} \qquad (A1.1)$$

where: S was the salinity at tree position and $S_{0.5}$ and d were species specific constants (Table A1.1). The function $f_n(RNA)$ was the growth multiplier considering the effect of the relative nutrient availability (RNA) on growth (Chen & Twilley 1998):

$$f_n(RNA) = c_1 + c_2 \times RNA + c_3 \times RNA^2 \qquad (A1.2)$$

where: c_1, c_2 and c_3 were species specific constants (Table A1.1).

Table A1.1. Growth and spatial competition species-specific parameters used in the KiWi model. Sources: (1) Chen & Twilley 1998, (2) see App. 2.

Parameter	Description	A. germinans	L. racemosa	R. mangle	
DBH_{max}	Maximum diameter at breast height	140	80	100	(1)
H_{max}	Maximum height	3500	3000	4000	(1)
G	Growth constant	162	243	267	(1)
b_2	Constant in height to dbh relationship	48.04	71.58	77.26	(1)
b_3	Constant in height to dbh relationship	0.172	0.447	0.396	(1)
d	Salinity effect constant	-0.18	-0.20	-0.25	(1)
$S_{0.5}$	Salinity effect constant	72.0	65.0	58.0	(1)
c_1	RNA effect constant	-0.50	-1.00	0.00	(1)
c_2	RNA effect constant	2.88	4.42	1.33	(1)
c_3	RNA effect constant	-1.66	-2.50	-0.72	(1)
a	FON radius scaling parameter for heterospecific competition parameterization	13.7	17.0	18.0	(2)
b	FON radius scaling parameter for heterospecific competition parameterization	0.72	0.95	0.83	(2)

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App. 2. Parameterization of the *FON* radius calculation.

In the KiWi model, the *FON* radius R of a tree depends on its size:

$$R = a \times RBH^b \qquad \text{(A2.1)}$$

where: a and b are scaling parameters. The parameterization of a and b can be effectuated to reproduce the *DBH*-density trajectories of a self-thinning phenomenon.

Demonstration:
In equation A2.1, the *RBH* is half the *DBH*, so A2.1 becomes:

$$R = a \times \frac{1}{2^b} \times DBH^b \qquad \text{(A2.2)}$$

The *FON* approach has been seen as reproducing the self-thinning trajectory very well (Berger & Hildenbrandt 2003). During the self-thinning in KiWi model, because of the mortality function, the total *FON* area of all individuals can be considered as constant since the dead individuals are replaced by growth of the remnant. This corresponds to a constant maximum resource use. Let assume this constant be FON_{tot}. We could simplify its calculation as:

$$FON_{tot} = N \times FON_{ind} \qquad \text{(A2.3)}$$

where FON_{ind} is the mean area of the *FON* area of the individuals defined as:

$$FON_{ind} = \pi \times R^2 = \pi \times a^2 \times \frac{1}{2^{2b}} \times DBH^{2b} \qquad \text{(A2.4)}$$

where R and DBH are respective mean values assuming they represent the entire community. Assuming that during self-thinning we have the relationship of the *DBH*-density trajectory:

$$\log(N) = \alpha + \beta' \log(DBH) \qquad \text{(A2.5)}$$

or

$$N = \exp(\alpha) + DBH^{\beta}$$

Interchanging Equation A2.4 in A2.3 and comparing to A2.5 we get:

$$N = \exp(\alpha) + DBH^{\beta} = \frac{FON_{tot}}{FON_{ind}} = FON_{tot} \times \left(\frac{2^{2b}}{\pi \times a^2} \right) \times DBH^{-2b} \qquad \text{(A2.6)}$$

Since $\exp(\alpha)$ and $FON_{tot} \times \left(\dfrac{2^{2b}}{\pi \times a^2} \right)$ are not dependents on *DBH*, we can link the β parameter directly to the *FON* b parameter:

$$\beta = -2b \qquad \text{(A2.7)}$$

Identically we can derive the value of a:

$$a = \sqrt{\frac{2^{2b} \times FON_{tot}}{\pi \times \exp(\alpha)}} \qquad \text{(A2.8)}$$

We determined with the KiWi model that FON_{tot} is constant ~215% and not depending on a nor b. These relationships are confirmed by simulation experiments with monospecific stands (Fig. A2.1).

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Parameterization of species-specific values

Data from monospecific stands of Belizean mangroves (I.C. Feller, F. Chi and C. Piou unpubl.) at different density were used to create regressions and calculate the parameters a and b for *Rhizophora mangle* and *Avicennia germinans*. Fig. A2.1 shows the field data, linear regression and results of monospecific simulation without recruitment with the corresponding *FON a* and *b*.
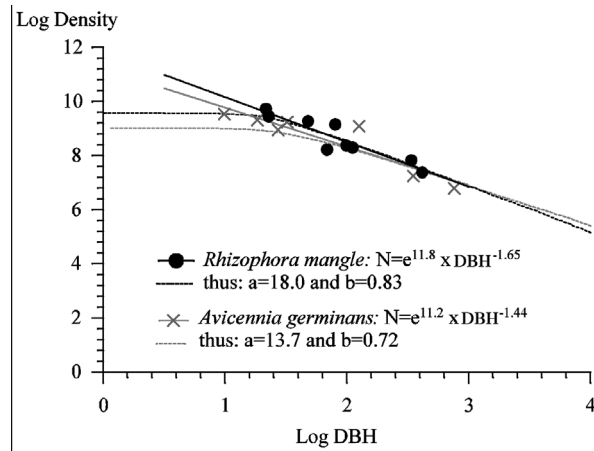

Fig. A2.1. Field DBH-density (cm and stem/ha) data on natural logarithmic scale with corresponding linear regression (plain lines) and simulation results (dashed lines) of monospecific stand of *Rhizophora mangle* (black) and *Avicennia germinans* (grey) without recruitment.
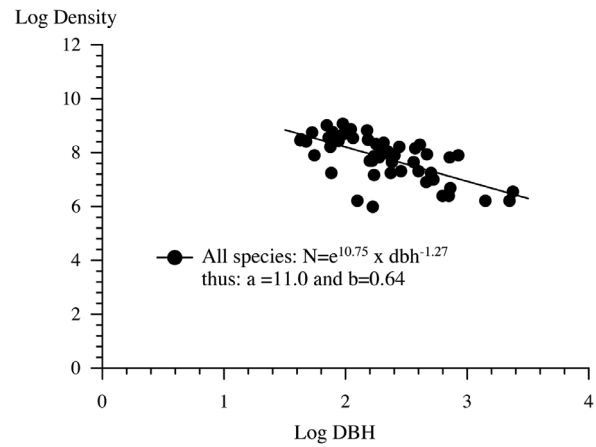
Fig. A2.2. CARICOMP DBH-density (cm and stem/ha) data of mixed forests on natural logarithmic scale with corresponding linear regression (plain line).

For *Laguncularia racemosa*, not enough monospecific field data were available, so we estimated that this species was less competitive in Belize in terms of spatially distributed resources such as light. This was then considered in the *a* and *b* parameter giving a larger *b*-value (0.95) and smaller *a*-value (17.0) than for *R. mangle* (e.g. Berger & Hildenbrandt 2003).

Parameterization of species-identical values

To use the same approach for the tuning of the a and b parameter in the first parameterization (*species homogeneous spatial competition*), data of density and mean diameter from mixed stands of the three species were considered. We used the data from plots of the CARICOMP program (CARICOMP 2002, http://www.ccdc.org.jm/mangrove_data.html) over the entire Caribbean region to create the regression and calculate the parameters a and b considering all three species (Fig. A2.2).

App. 3. Sensitivity analysis on random variables affecting recruitments

Since there are no solid data on the variation of sapling numbers, the ranges of the two random variables rnd_1 and rnd_2 (Eq.5) were arbitrarily chosen (respectively [0.5 to 1.5] and [0.1 to 0.3]). They described a natural fluctuation and occasional reappearance of saplings in the plot respectively. In order to analyze the suitability of these parameterizations, a sensitivity analysis was conducted to test the effect of the variation of these ranges on the variation of the median values of index of species dominance heterogeneity (I_{SDH}).

For this analysis, we selected simulations with the *species heterogeneous spatial competition* parameterization, the intermediate abiotic conditions and three selected cases of perturbation regimes that should present the so-called bell-shape pattern characteristic of the intermediate disturbance hypothesis. For each case, we tested 11 different new ranges for each random variables by multiplying the limit values of these 2 ranges by variation factors of $\Delta rnd = 0.5$ to 1.5. We measured the median I_{SDH} results over the last 400 years for each new range ($I_{SDH\text{-}new}$) and analyzed the variation comparing it to the original value ($\Delta I_{SDH} = I_{SDH\text{-}new} / I_{SDH\text{-}0}$).

The results of this sensitivity analysis are presented in Fig. A3.1. Variations of up to 10% of the ranges of rnd_1 and rnd_2 change with less than 10% the I_{SDH} results and not generally the original pattern of system answer to perturbation regime. Actually, only with the extreme perturbation regime the rnd_2 variation lead to variations of I_{SDH} higher than 5% but increasing then the trend of bell-shape answer of the system to perturbation regime.

Based on these results, we considered the selected ranges of rnd_1 and rnd_2 adequate for our study.
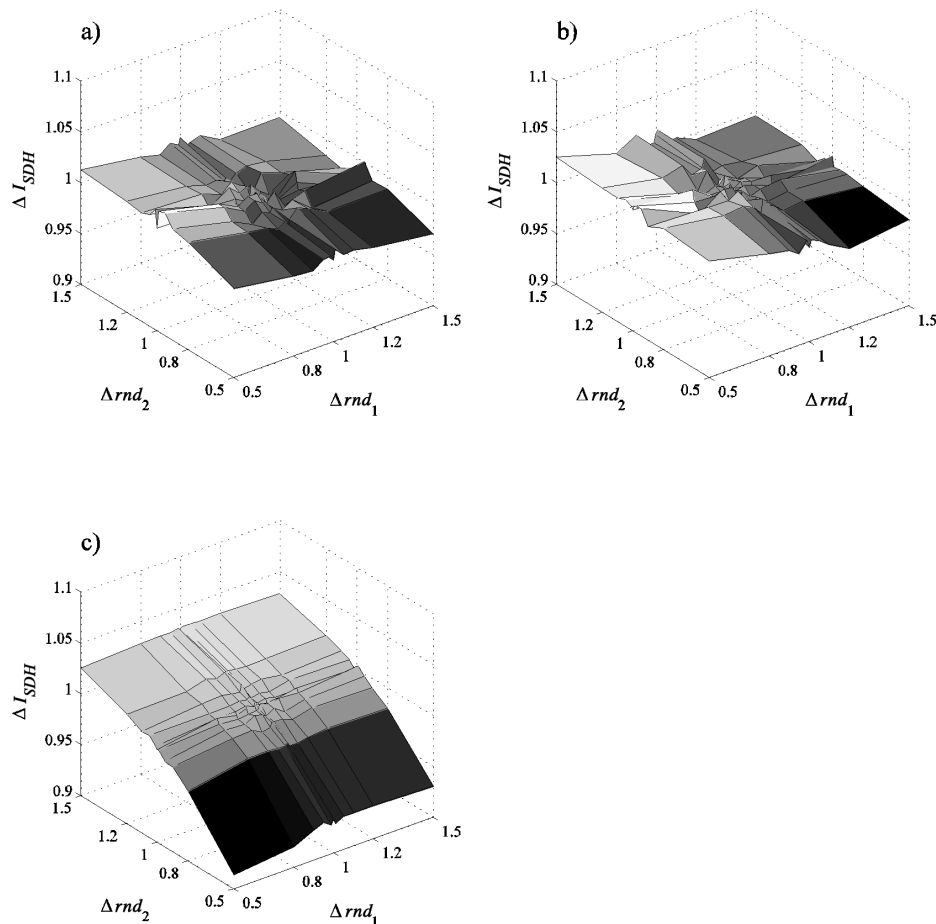

Fig. A3.1. Results of sensitivity analysis of rnd_1 and rnd_2 on I_{SDH} variations, (**a**) with low perturbation regime (intensity = 30%, frequency = 1 / 100 yr), (**b**) with intermediate perturbation regime (intensity = 50%, frequency = 1 / 40 yr) and (**c**) with extreme perturbation regime (intensity = 99%, frequency = 1 /10 yr) (original values of I_{SDH}: 2.551, 2.781 and 2.766 respectively). All sensitivity analysis simulations were done with the *species heterogeneous spatial competition* parameterization and intermediate abiotic conditions.

App. 4. Complementary results

    In this appendix we present complementary results of the simulation exercises. Fig. A4.1 shows the general results of the first analysis: relative nutrient availability and salinity conditions on species dominance heterogeneity.

    Fig. A4.2 shows specific results of the second analysis: effects of perturbation regimes on species dominance heterogeneity with selected abiotic scenarios.
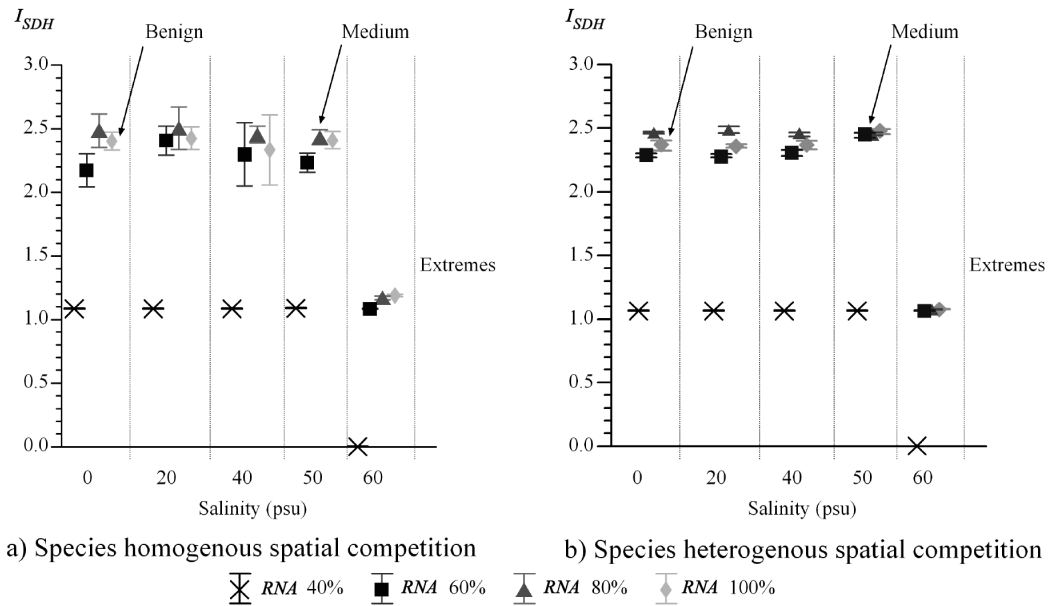

Fig. A4.1. I_{SDH} variations according to salinity and relative nutrient availability (*RNA*) conditions for the two competition parameterizations. Points are median values of replicate simulations, error bars represent first and third quartiles.
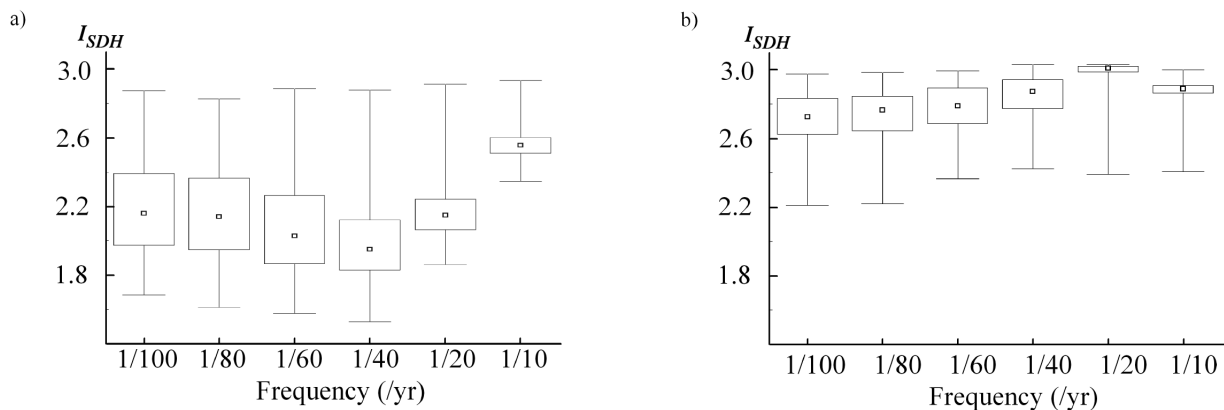

Fig. A4.2. Median I_{SDH} variations following perturbation frequency for the two competition parameterizations (**a** and **b**) with selected mortality intensity (70%) and medium abiotic scenario (Salinity 50 and *RNA* 80) (*N* = 30 for each point, boxes represent first and third quartiles, error bars represent minimum and maximum).

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The analysis of variations in species diversity (I_{SDH}) of the system depending on the perturbation regime showed different type of patterns for the different parameterizations (Fig A4.3). The *homogeneous spatial competition* parameterization with benign abiotic conditions led to 4 U-shaped patterns out of 11 analyses. The *heterogeneous spatial competition* parameterization with benign abiotic conditions led to 4 bell-shaped patterns out of 11 analyses. In both cases, the rest of the analyses showed irregular, increasing or decreasing pattern of I_{SDH} variations. With medium abiotic conditions the patterns were more often U-shaped or bell-shaped, but with an identical trend: the *homogeneous spatial competition* parameterization led to 6 U-shaped patterns and the *heterogeneous spatial competition* led to 7 bell-shaped patterns out of 11 analyses in both cases.
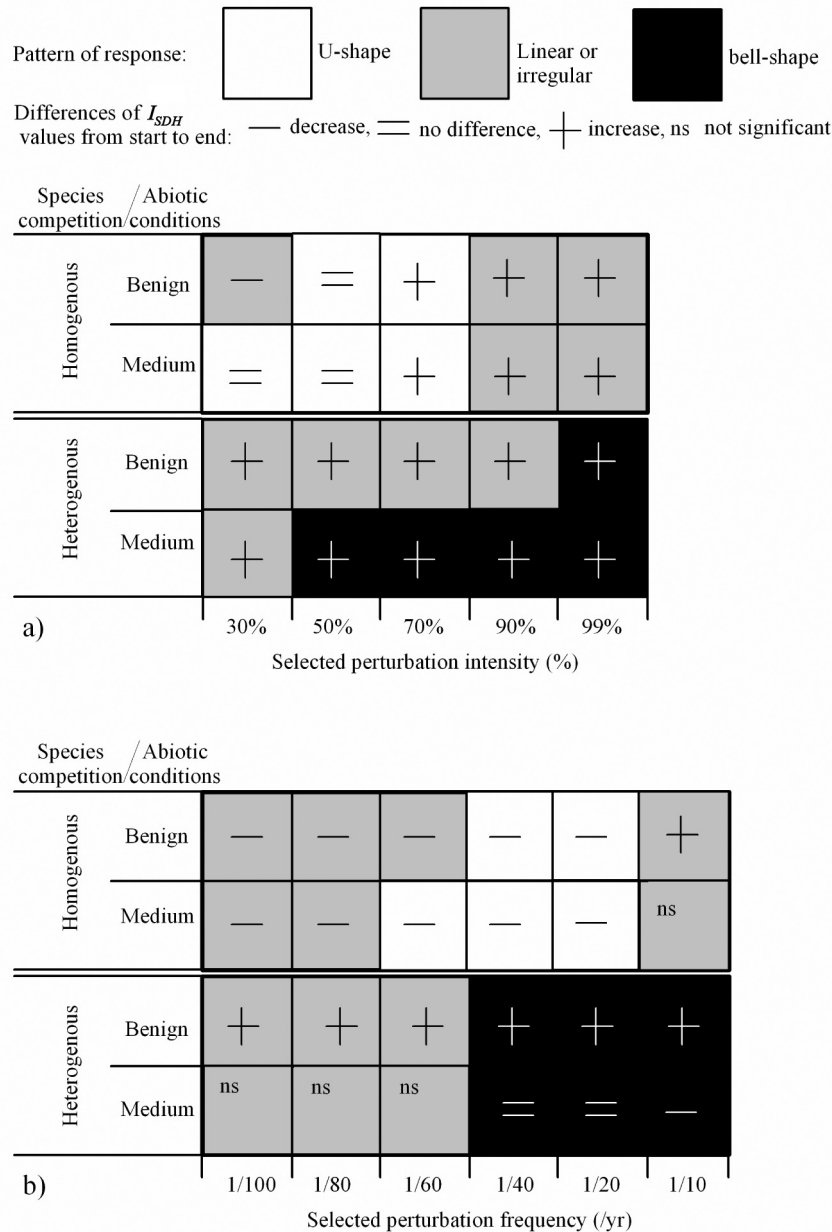

Fig. A4.3. Patterns of system response in median I_{SDH} variations according to frequency effect with selected intensity of disturbance (**a**) or according to intensity effect with selected frequency of disturbance (**b**).

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