

Can disturbance be responsible for maintaining diversity in biological communities? Predictions from a community model with varying degrees of disturbance and demographic stochasticity

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Abstract

The Intermediate Disturbance Hypothesis (IDH) is one of the leading ideas to explain the maintenance of diversity in biological communities. It was proposed in the theoretical context that communities under linear competition were fated to have only one species as an outcome of sequential competitive exclusions. According to the IDH, intermediate degrees of disturbance can increase the time of coexistence among species by periodically resetting competition outcomes and then avoiding communities to reach equilibrium. Here we investigated if stochasticity in the birth and death process may change diversity-disturbance relationship in communities under linear competition and varying degrees of disturbance. We also investigate if mortality aggregated in time, as disturbance is usually defined, is equivalent to increase the per-capita mortality rate with the average mortality effect of disturbance. To analyze the effect of disturbance, we implemented a simulation model of multiple species with intra-interspecific competition under a varying regime of disturbance. We found that when demographic stochasticity is included in the model the IDH pattern disappear. Disturbance keeps being important to define diversity but on contrary to the stated by IDH; the effect is only negative with disturbance being unable to prolong species coexistence with extinction increasing with disturbance. Since extinctions happens even without disturbance we underlines the role of dispersal as a primary ecological process to the maintenance of diversity. Finally, we highlight the importance of considering demographic stochasticity in studies of impacts of disturbance. since we have demonstrated that it may change the predictions from those of deterministic models.

Introduction

How diversity is maintained in ecological communities is one of the most important questions in ecology. Simple linear models of species competition such as the Lotka-Volterra model predicts that the best competitor will exclude all the other species. Coexistence can

occur only if intraspecific competition is stronger than interspecific effects. Even so the maximum number of coexisting species is given by the number of niche axes [1]. Hence, as a corollary of the principle of competitive exclusion [2], all the communities where there are competitive asymmetries among species, should have only a few dominant species left. In this context, a leading idea about how the diversity is maintained is a non-equilibrium proposal: the intermediate-disturbance hypothesis, IDH [3].

Disturbance, defined as any density-independent process that removes biomass or individuals from the community was first proposed in the 1970's [4–6] as a mechanism that promotes coexistence among species and consequently the maintenance of biodiversity in communities. The IDH states that intermediate disturbance prevents the community to reach equilibrium and then the exclusion of species by the dominant ones [5, 7]. At low levels of disturbance, the community reaches the equilibrium and only the best competitors persist; at too high or frequent disturbance only a few species resist after every disturbance event. Thus, according to the IDH, at intermediate intensities or frequencies of disturbance the eventual removal of individuals would reset the competitive dynamic to a scenario closer to the initial conditions, before the competitively weak species are excluded. The peak of diversity, then, should occur at intermediate intensities and frequencies of disturbance.

Despite its popularity, there is a harsh debate around the IDH and its operation [8–13], and no consensus about its validity has been reached. In a review of the IDH literature Mackey and Currie [14] found that the peak in diversity at intermediate levels of disturbance is not as ubiquitous as expected. Furthermore, the very own theoretical basis of the hypothesis is now under critique [13, 15] to the extent that some authors [13, 16] recently proposed the exclusion of disturbance from the list of ecological mechanisms that promote diversity. One of the arguments [13] is that the only effect of the disturbance is to slow down the per-capita growth rate of competing species, and thus increasing time to reach equilibrium, but not changing the equilibrium state of competitive exclusion by the best competitors. Indeed, Huston [6] simulating periodic disturbance in a deterministic dynamic of Lotka-Volterra competition model found that the perturbations only prolonged the transient period towards competitive exclusion. Some other theoretical models of disturbance predict a peak of diversity depending on the level of disturbance [15], but theoretical literature on IDH did not explore or even mentioned one of the most basic and inherently presented traits of biological population: the stochasticity of the birth-death process.

When considered in models of community dynamics, demographic stochasticity is able to produce some empirical patterns [17]. Here, we investigate if demographic stochasticity may change the competitive outcomes under different disturbance regimes relative to deterministic models adopted by the traditional theoretical approach of IDH. Demographic stochasticity promotes a random walk in species abundance where extinctions occur even when the per-capita birth rate is higher than the per-capita death rate. Since stochastic birth and death dynamics is inherent to dynamics of any biological population, and since

it can decrease community diversity, it is of central importance to investigate the effects of disturbance when community has demographic stochasticity. Further, we also investigate if mortality aggregated in time — as disturbance is usually defined — has the same effect of increase the per-capita mortality rate with the average value of a disturbance effect as proposed by [13].

We believe that a better understanding of the theoretical predictions from IDH and the role of disturbance on communities diversity is central not only for the advance of theoretical ecology but also for the understanding of how disturbance can affect biodiversity as disturbance regimes are changing faster due to human activities, with profound effects on ecosystems [18]. To evaluate the effects of demographic and disturbance stochasticity, we implemented a simulation model of multiple species with intra–interspecific competition under varying frequencies and intensities of disturbance.

Materials and Methods

To simulate the dynamics of birth and death in communities under varying disturbance regimes we used the algorithm of Gillespie [19] implemented in C++. This algorithm was proposed to simulate stochastic dynamics in continuous time in a approximation to the time in deterministic models. Each event has a specific rate of occurrence, so that they are independent events, with time of occurrence following an exponential distribution. The alternative and exclusive events that should occur at each time step are: birth of a single individual, death of a single individual or disturbance. An event of disturbance was simulated by removing a proportion of the individuals present at the current time of simulation; the disturbance regime was controlled by its occurrence rate. The simulation model has a total of seven input parameters (table 1), plus the matrix of coefficients of interaction. Here, the interaction coefficients were all negative (competition) in order to keep within the theoretical core of the IDH.

Simulation

In each step of simulation only one of the three events (birth, death and disturbance) can take place and the probability of each event depends on its rates. The disturbance rate is constant and independent from the number of individuals in the community. The per-capita death rate is constant and its value varies among species, following a normal distribution. Since the rate is the same for all individuals of each species, the probability of a death in a population is proportional to the product of the death rate and the population size.

The per-capita birth also varied among species and was the only rate that is not constant along time in the model. It depends on the maximum per-capita birth rate defined for the species i , the number of individuals of the species i and of the other

species. The effect that the remaining species have on the species i is defined by the coefficients of competition and the abundance of the other species. The effect is linear, as in a classical Lotka-Volterra competition relationship. In each time step, then, the per-capita birth rate of species i is:

$$b_i = b_{i\max} - \left(\frac{b_{i\max} - d_i}{K_i} \right) \sum_j^S a_{ij} N_j \quad (1)$$

,where S is the number of species, a_{ij} are interspecific competition coefficients and N_j species abundances. Thus, in the absence of competitors — from individuals of its own species or others — the per-capita birth rate, b_i , assumes its maximum value, $b_{i\max}$. The probability of a birth in a population is proportional to the updated per-capita birth rate times the population size. The interspecific competition coefficients taken from a uniform distribution between -1 and 0, thus all species are competitors at some degree. Intraspecific competition coefficients were set to minus one.

Once rates are defined, we performed the following steps in order to make an event happen: (a) for each species a value is taken from an exponential distribution, which the parameter rate is the sum of the birth and death rate of the species. Thus, each species will have a value representing the minimum time the population would take to have one death or one birth. Likewise, a value of time is taken from an exponential distribution to the disturbance event, also with parameter value of the distribution equals the value of the disturbance rate. (b) The smallest time value determines if the next event will be a disturbance or a demographic variation in one of the species. (c) If disturbance has the shortest time, a fraction I of the entire community is removed. The probability of an individual to be removed by the disturbance is independent of the species it belongs. Still, a birth or a death is drawn at random for the population with the shorter time. The probability of the event to be a birth or a death is proportional to the corresponding rates. If death is drawn, one individual of the population is removed, and if birth is drawn, one individual is added to the population. (d) The time of the event that just happened is summed to the total elapsed.

We treated our simulations as virtual experiments, in which we have three conditions: (1) control; (2) treatment with continuous mortality — treatment 1 and (3) treatment with aggregated mortality — treatment 2 (table 2). The first condition is a traditional control, where all the non-interesting parameters are maintained with the same values of the treatments and the effect to be analyzed is absent. In this case, then, the control condition lacks disturbance. This kind of control is the one usually adopted by proposals and theoretical researches in IDH [6, 15]. Our condition (2) is what Fox [13] proposes to be the control in IDH. Here we named it as treatment with continuous mortality because the effect is present by modifying the per-capita mortality rate, as constant disturbance. Finally, the third condition is the disturbance treatment itself. It is the condition usually used in theoretical and experimental-observational tests of diversity-

disturbance relationship.

At the simulations, then, to perform the control we kept all the other conditions equal and we set the two parameters of disturbance, frequency (F , the rate at which a disturbance occurs) and I (intensity, the proportion of individuals removed), to zero. At the treatment with continuous mortality the parameters F and I were set to zero, and the averaged effect of disturbance, calculated by the product of F and I , was added to the intrinsic mortality rate of the species. Therefore, the effect of disturbance was included as an increase in the mean mortality rate (table 2 to see how the average effect of disturbance is calculated). For the treatment of aggregated mortality, disturbance acts by removing a proportion I of the total of individuals at a certain frequency F . Thus in this condition, the parameters F and I vary according to the method described in the next section. All the three conditions was simulated 500 times to each combination of parameters, and the mean value was used to analyze the effect of disturbance.

For each combination of parameters, we first ran the control and recorded the time elapsed for 80% of the populations went extinct. Afterwards we ran the two treatment simulations for the same time. The general effect of each treatment was evaluated as the difference in the proportion of remaining species in comparison to the control.

Input parameters values

We defined the values of parameters with the Latin Hypercube Sampling (LHS) method [20], a method of parameter space exploration. This method is a solution to the problem of high costs of computer processing time when running models with all possible combination of parameter values, which can be infinite when the parameters are continuous. Unlike the approach of full parameter space exploration, in the LHS method we take N samples from the parameters space without replacement. Each sample has a singular combination of parameters to be use to run the model. The size N of the sample may be defined by an adaptative sampling refinement [21]. It can be done by increasing N systematically and comparing if the relation among outputs of the simulations and parameters remains constant with sensitivity analysis. Here, we have made this comparison by Symmetrized Blest Measure of Association (SBMA), which shows the concordance between different N . The LHS is a representative sample of a given parameter space, which allows to draw valid inferences about the whole universe of responses of simulations trough standard statistical analyses [21].

After defining the input parameters, the first step when using the LHS method is to define the probabilities distribution functions (pdfs) of the parameters (table 1) in order to define the parameter space to be sampled. As each species has its own basal birth rate ($b_{i\max}$) at the LHS, we defined the mean and standard deviation of the normal distribution to be used in simulations in which the $b_{i\max}$ rates were drawn. The mean and standard deviation of $b_{i\max}$ followed an uniform distribution. To assure that the intrinsic death rate was always smaller than the maximum birth rate, at the LHS it was expressed

as a proportion of the maximum intrinsic birth rate of the species. This proportion also followed a uniform distribution. The frequency of disturbance (F) which was a proportion of the intrinsic death rate, followed a lognormal distribution. The other two remaining parameters — I and K — followed uniform distributions. Afterwards, we have applied a single-switch-optimized sample reordering scheme [22], in order to guarantee that the input parameters values are not correlated with each other. We took 200 values from each distribution. We also took 100 values and obtained satisfactory results from the SBMA analysis, with correspondences around 0.8, showing that an hypercube with 200 combinations of values was an adequate sample of the model parameter space.

Statistical analyses

Finally, we performed generalized linear regression with binomial errors to look for general tendencies such as (a) find the important effects (b) identify the signal of the effects (c) compare treatments outputs. The results analyzed were those obtained from the simulations of the treatments conditions, since the control was forced to be constant relative to any parameter (i.e. proportion of remaining species equal to 0.2) and thus independent of any input parameter. The response variable in regression models was the proportion of remaining species relative to the initial richness. The predictor variables were the input parameters of the simulation models, the kind of treatment and also the interactions among treatment and disturbance parameters. Since any correlation among parameters was excluded, the coefficients of the model estimates the additive effects of each variable. Hence, we use confidence intervals of the coefficients to express the sensitivity of simulation results to each parameter. We also performed an uncertainty analyses through the comparison of the empirical cumulative distribution function (ecdf) of the results of the control and treatment simulations.

All the statistical analyses and graphics were performed and generated in the R environment, version 3.0.1 [23]. We have used the package under construction `pse` (current version available online [24]) which uses the following R packages: `Hmisc` [25], `sensitivity` [26] and `car` [27].

Results

On contrary to the IDH and other predictions found to the disturbance-diversity relationship, in our stochastic model the disturbance had a consistently negative effect on diversity, regardless of the degree or frequency of disturbance we analyze. While in the control simulations, the remaining species was set to 0.2 of the original richness, both treatments simulations kept that proportions consistently above 0.2 (figure 1). These results show that disturbance not only is unable to keep more species for a determined period of time but also that it promotes an increase in extinctions rates when compared with the scenarios without disturbance.

Besides the two conditions of disturbance — aggregated (treatment 2) and continuous (treatment 1) in time — resulted in a decrease in species coexistence, when the disturbance was aggregated, a larger proportion of the results were of total extinctions or values above the control when compared with the condition of continuous disturbance (figure 2). In the regression, disturbance had significant negative effect on the proportion of remaining species in both treatment conditions (figure 3). Additionally, the kind of treatment had significant interaction with the parameters F and I (figure 3). Disturbance as aggregated mortality increased the negative effect of disturbance on the proportion of remaining species when compared with the disturbance as continuous mortality.

Both intensity and frequency of disturbance had a negative effect on the proportion of species remained, but intensity (I) had an stronger effect (figures 3). Two other parameters had significant negative influences on the maintenance of species in communities under disturbance (figure 3). Those parameters are both demographic rates: mean of the maximum per-capita birth rates (b_{imax}) and the death rates (d).

Discussion

According to the Intermediate Disturbance Hypothesis (IDH), disturbance — in an intermediate level — is able to increase the time of coexistence among species under a linear competition dynamic [5, 6]. Other theoretical models showed that the shape of the disturbance-diversity relationship can vary [15], but the positive correlation is one of the possible outputs. We have shown that when stochastic demography is included in the model, the effect of disturbance is always negative, due to an increase in extinctions rates. This result extends the critics to IDH in two important ways: (1) The effect of disturbance on diversity is neither positive as stated by the IDH nor a mere increase in average per-capita death rate, as proposed by previous critics to IDH; (2) as a product of ecological drift, this effect depends only of population sizes and not whether competitive interactions follow linear or non-linear relationships.

Ecological drift can be defined as the random walk of species abundances [17, 28] due to stochastic births, deaths and migrations. For allowing sequential events of death and births, ecological drifts promotes oscilation in the system with decrease in species diversity, with time of species extinction proportional to the size of populations [29, 30]. That dependency on the size is due to the fact that sequential events of death represent different proportion of the whole, depending on the size of the system. Thus, competition is not the only process that can decrease the number of coexisting species, ecological drift also does. However, the leading mechanisms are very different. That differences can make the system respond differently when exposed to the same stimulus; in our study this stimulus is disturbance. Disturbance here removes in a single step a proportion of the individuals (treatment 2) or increase the per-capita death rates (treatment 1). In a stochastic birth-death dynamics both effects increase the probability of sequential death

events that can drive a small population to extinction. Accordingly, our results show that disturbance operated differently from what had been found in previous studies in which only deterministic competition was considered in the models. Huston [6] when simulated disturbance in a system with two competing species found that the disturbance in a certain frequency increased the transient period. In our simulations, on contrary, disturbance has the effect to speed up and not slow down the transient to equilibrium. Miller et al [15] when varying the intensity and frequency in a system with two competing species also found results much different from ours. They found an interaction between the frequency and intensity, and depending on the combination of them, disturbance promotes coexistence.

Disturbance in our simulation, then, had an equivalent effect of sequential death events — which is what promotes extinctions in communities under drift. The length of this sequence depended on parameter I and the time between disturbances depended on the parameter F . And since intensity had a stronger effect than the frequency of disturbance, the length of death sequence is more important than the rate of this events to promote extinctions. Nevertheless, there was a considerable difference between the two disturbance treatments. When many individuals were removed in single events of disturbance more extinctions occurred than at the treatment where the disturbance was an increase in death rate. Moreover, there is an interaction between the kind of treatment and the disturbance parameters, with the treatment of aggregated mortality increasing the negative effect of disturbance. This result indicates that disturbance promotes more extinctions when individuals are removed at once. That is because removals of individuals aggregated in time is a long sequence of death events, while an increase in the death rate only raises the probability of such a sequence. Thus, on contrary to expected [13], the effect of disturbance is not merely an increase in the mean death rate, it has the effect of accelerate the extinction rates even more.

Further, although disturbance is independent of populations size it is the smallest populations that become more prone to disappear after (or during) an event of disturbance. That is because their extinction probabilities that were already high due to their small sizes, get even higher after the removal of individuals. In this context, since inferior competitors tend to have smaller population than best competitors because of the process of competition itself, when disturbance affect mostly the rare species, it has the side effect of magnifying competition effects. This effect of increase competitive asymmetries is another outcome contrary to the stated by the IDH [6, 31], in which disturbance would weaken competition strength [6, 31], acting as stabilizing factor (*sensu* [32]). Therefore, disturbance speeds up the system towards the equilibrium of low diversity not only for the ecological drift process but also for competition.

In our simulations even in control situation the extinction rate was larger than zero because (1) we aimed to promote deterministic competitive exclusion and thus set an interaction with high conectance and high mean values of competition coefficients; (2) we included demographic stochasticity, which in closed communities promotes a monotonic

loss of species due to stochastic extinctions. Thus, even with no disturbance, a process of replacement of extinct species would be necessary to maintain diversity. In community models with stochastic births and deaths the usual solution is to include immigration from some source pool [17,33], in which the immigration rate must balance the extinction rate.

When the disturbance is present, then, the immigration rate should be higher than when disturbance is absent. Higher immigration and extinction rates, on the other hand, promotes higher turnover of species in time. Therefore, in communities where there is high level of disturbance, one should expect that the rate of substitution of species to be high in order to maintain the biodiversity. Moreover, if we include immigration in our models and if the worst competitors are best colonizers the competitive asymmetries can be attenuated. Even so, immigration *per se* could only maintain an equilibrium diversity in communities, but it is not able to produce the IDH patterns. Maybe if the immigration rates have a positive correlation with the extinction rates until a certain threshold the IDH patterns appear. If so, at low level of disturbance the flux of immigration will be low and then few new species will enter in the community and in too high level of disturbance the extinction rate will be above the threshold and the immigration will not be enough to overcompensate the loss of species. With this, at intermediate level diversity will be maximized, but although the pattern of diversity-disturbance be the same of the IDH, the leading mechanisms are completely distinct. Moreover, there is not any evidence indicating that immigration rates are related to extinction rates, although some model of zero-sum such as Hubbell's neutral model of diversity [17] has this correlation as an implicit assumption. And if such dependency of immigration rate on extinction rate does not exist, the only way to have the IDH pattern is by colonization-competition trade-offs where the interaction among species are not linear relations [10,16,34] and then are beyond the scope of the original proposal of IDH [13].

We conclude that being the effect of disturbance always negative in a linear competition model with stochastic birth and death, intermediate levels of disturbance should be put aside as a mechanism that promotes coexistence among species in this kind of dynamic. Considering this, we highlight the fact that the process of birth and death is inherently stochastic — or that a stochastic approach is what best describes the process. Therefore, stochasticity can not be ignored in studies of impacts of disturbance or environmental fluctuations on biodiversity, which effect can be much more dramatic than ecologists usually consider.

Sobre a segunda frase: na prática, não na teoria, né?

Não entendo muito bem porque a IDH não está relacionada com o trade-off colonização - competição

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References

1. Tilman D (1982) Resource competition and community structure, volume 17. Princeton University Press.
2. Gause G (1934) The struggle for existence. The Williams Wilkins company.
3. Wilson JB (1990) Mechanisms of species coexistence: Twelve explanations for hutchinsons paradox of the plankton: evidence from the new Zealand aplant communities. *New Zealand Journal of Ecology* 13: 17–42.
4. Horn H (1975) *Ecology and Evolution of Communities*, Cambridge: Belknap press, chapter Markovian properties of forest sucesion.
5. Connell JH (1978) Diversity in Tropical Rain Forests and Coral Reefs: High diversity of trees and corals is maintained. *Science* 199: 1302–1310.
6. Huston M (1979) A general hypothesis of species diversity. *American naturalist* 113: 81–101.
7. Grime JP (1973) Competitive exclusion in herbaceous vegetation. *Nature*, UK 242: 344–347.
8. Padisak J (1994) Identification of relevant time-scales in non-equilibrium community dynamics: Conclusions from phytoplankton surveys. *New Zealand Journal of Ecology* 18: 169–176.
9. Wilson JB (1994) The intermediate disturbance hypotheses of species coexistence is based on patch dynamics. *New Zealand Journal of Ecology* 18: 176–181.
10. Chesson P, Huntly N (1997) The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *American Naturalist* 150: 519–553.
11. Dial R, Roughgarden J (1998) Theory of marine communities: the intermediate disturbance hypothesis. *Ecology* 79: 1412–1424.
12. Sheil D, Burslem DF (2003) Disturbing hypotheses in tropical forests. *Trends in Ecology & Evolution* 18: 18–26.

13. Fox JW (2013) The intermediate disturbance hypothesis should be abandoned. *Trends in ecology & evolution* 28: 86–92.
14. Mackey RL, Currie DJ (2001) The Diversity-Disturbance Relationship: Is It Generally Strong and Peaked? *Ecology* 82: 3479–3492.
15. Miller AD, Roxburgh SH, Shea K (2011) How frequency and intensity shape diversitydisturbance relationships. *Proceedings of the National Academy of Sciences of the United States of America* 108: 5643–5648.
16. Roxburgh S, Katriona S, Wilson J (2004) The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. *Ecology* 85: 359–371.
17. Hubbell S (2001) The unified neutral theory of biodiversity and biogeography. Princeton: Princenton University Press, 375 pp.
18. Turner M (2010) Disturbance and landscape dynamics in a changing world. *Ecology* 91: 2833–2849.
19. Gillespie DT (1976) A general method for numerically simulating the stochastic time evolution of coupled chemical reactions. *Journal of Computational Physics* 22: 403–434.
20. McKay M, Beckman R (1979) A comparison of three methods for selecting values of input variables in the analysis of output from a computer code. *Technometrics* 21: 239–244.
21. Chalom A, de Prado P (2012) Parameter space exploration of ecological models. arXiv preprint arXiv:12106278 : 1–37.
22. Huntington D, Lyrantzis C (1998) Improvements to and limitations of latin hypercube sampling. *Prob Engng Mech* 13: 245–253.
23. R Core Team (2013) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
24. Chalom A, de Prado PIKL (2013) pse: Parameter space exploration with Latin Hypercubes. URL <http://ecologia.ib.usp.br/let/doku.php?id=engl:tutorials:rcode>. R package version 0.2.0.
25. Jr FEH, with contributions from Charles Dupont, many others (2013) Hmisc: Harrell Miscellaneous. URL <http://CRAN.R-project.org/package=Hmisc>. R package version 3.12-2.

26. Pujol G, Iooss B, Janon A (2013) sensitivity: Sensitivity Analysis. URL <http://CRAN.R-project.org/package=sensitivity>. R package version 1.7.
27. Fox J, Weisberg S (2011) An R Companion to Applied Regression. Thousand Oaks CA: Sage, second edition. URL <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>.
28. Vellend M (2010) Conceptual synthesis in community ecology. *The Quarterly Review of Biology* 85: 183–206.
29. Renshaw E (1991) *Modelling Biological Populations in Space and Time*. Cambridge University Press.
30. Haegeman B, Loreau M (2010) A mathematical synthesis of niche and neutral theories in communityecology. *Journal of theoretical biology* 269: 150–165.
31. Violle C, Pu Z, Jiang L (2010) Experimental demonstration of the importance of competition under disturbance. *Proceedings of the National Academy of Sciences of the United States of America* 107: 12925–9.
32. Adler PB, HilleRisLambers J, Levine JM (2007) A niche for neutrality. *Ecology Letters* 10: 95–104.
33. Caswell H (1976) Community structure: A Neutral model analisys. *Ecological Monographs* 46: 327–354.
34. Kondoh M (2001) Unifying the relationships of species richness to productivity and disturbance. *Proceedings of the Royal Society of London B* 268: 269–271.

Tables

Table 1. Parameters of the simulation models and matrix of coefficients of inter – specific competition

Symbol	Meaning	Value
S	Initial species richness	$S \in [2, 201]$
$n0$	Initial population size, equal for all the species	$n0 \in [2, 201]$
$b_{i\max}$	Maximum per-capita birth rate of species. It is the rate which each individual is born, by unity of time, at maximum; it is the intrinsic birth rate in absence of competitors. The realized intrinsic birth rate, b , decreases linearly with the effect of competitors at the community (equation 1)	$b_{\max} \sim \text{Normal}(\text{mean} \in [0.01, 1], \text{sd} \in [0.01, 1])$
d_i	Per-capita death rate of each species; the rate at each individual of a species dies by unity of time. At the model it is a proportion of the mean $b_{i\max}$ in order to guarantee an intrinsic increase rate positive in absence of competitors	$d \in [0.01, 1]$
K_i	Species support capacity	$K \in [5, 100]$
I	Proportion of individuals of the community to be removed at each event of disturbance	$I \in [0.001, 1]$
F	Frequency of disturbance that an average individual suffers during life. It is then a proportion of the average intrinsic mortality rate. To take the disturbance rate, then, we multiply F by d	$F \sim \text{Lognormal}(\log\text{-mean}=0.0001, \log\text{-sd}=2)$
a_{ij}	Coefficients of competition among species	$a_{ij} \sim \text{Uniform}(\text{from}=-1, \text{to}=0) \text{ for } i \neq j \text{ and } a_{ij}=-1 \text{ for } i = j$

All the parameters followed a uniform distribution, except for F ; in LHS method b_{\max} was represented by the mean and standard deviation (sd) because the b_{\max} of each species was taken from a normal distribution when the community was generated in the simulations. The parameter F followed a lognormal distribution in LHS method, with defined parameters.

Table 2. The three condition of simulation and the value of parameters that differ among them

Simulation Condition	F	I	d
Control	0	0	d
Treatment with continuous mortality (treatment 1)	0	0	$d + (F \times I)^*$
Treatment with aggregated mortality (treatment 2)	F	I	d

* $F \times I$ is the average effect of disturbance: the average number of individuals killed per individual (a per-capita value) per time. That is because I is a proportion, and then a per-capita value, and the inverse of F is the mean time of occurrence of a disturbance.

Figure Legends

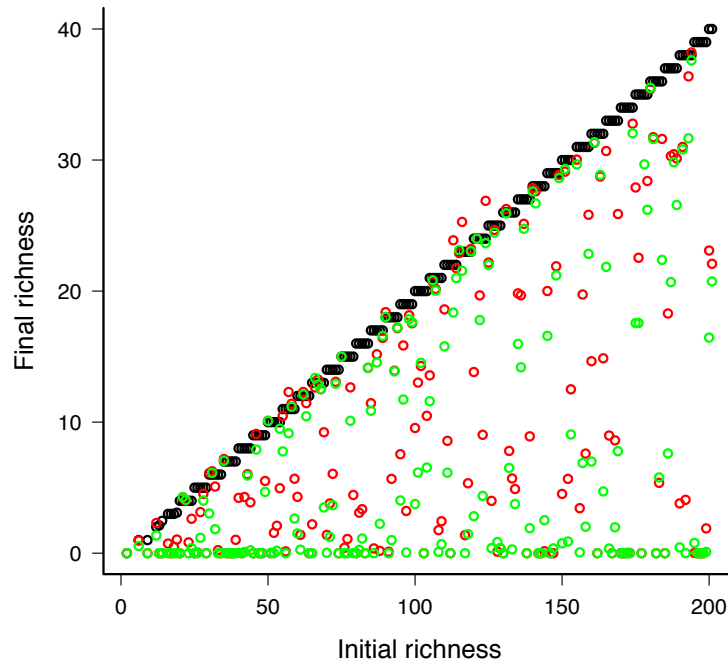


Figure 1. Mean values of the number of remaining species according to the initial number of species The black points are the results of the control conditions where disturbance is set to zero; the red dots are the results of scenario where the disturbance is continuous in time, with the addition of the average effect of disturbance directly on the intrinsic death rates; the green dots are the results of the simulations with disturbance as removal of proportion of the individuals at once, under a certain rate of occurrence.

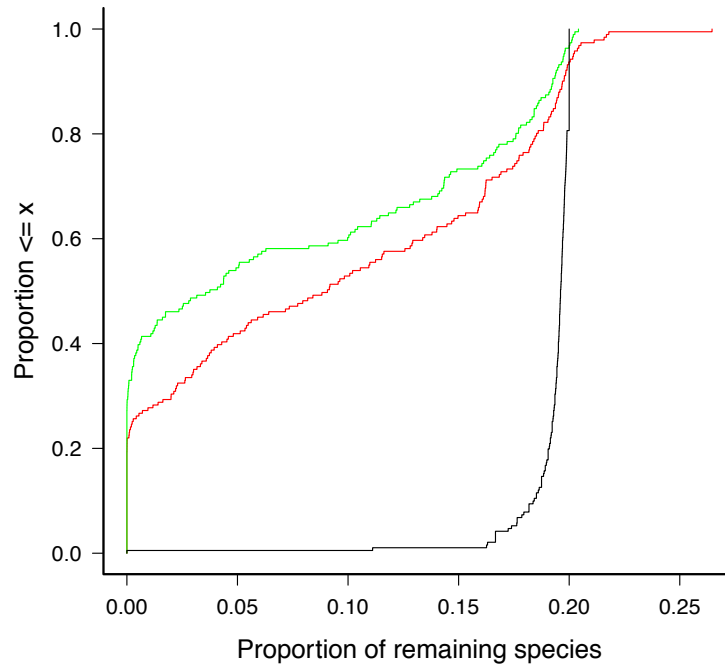


Figure 2. Empirical cumulative distribution function: distribution of the proportions of species remained from the initial richness in simulations Each line represents the proportions of species that remained relative to the number of species at the beginning of the simulation running in each condition: (a) green line is the results of the simulations of the treatment scenario with the disturbance aggregated in time; (b) red line is the results of the simulations of the treatment scenario with the disturbance continuous in time; an increase in the intrinsic death rate of the species present; (c) black line is the results of the control condition, in which the simulations ran until the community reached 0.2 of initial richness; that is why the line rises abruptly when 0.2.

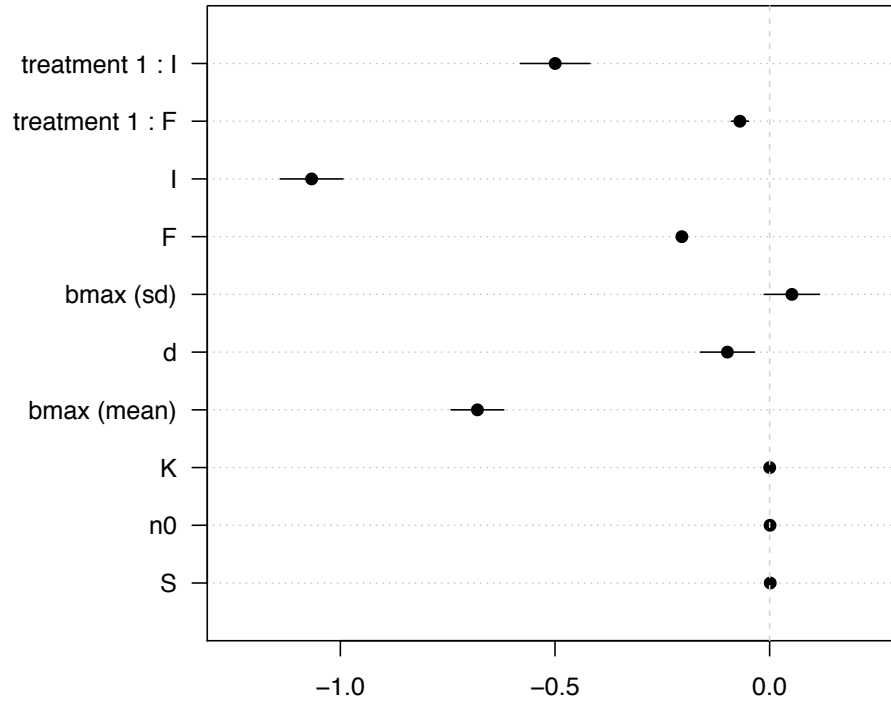


Figure 3. Effects, with respective confidence interval (0.95), of each parameter, and the interaction between treatment and disturbance, on the probability of permanency of species estimated by a generalized linear model with binomial errors. Disturbance — in terms of I and F — has negative values of coefficient relative to its effect on the proportion of species remaining on the community relative to the richness at the beginning of the simulations runs. However, the magnitude of the effect of disturbance depends on the type of treatment; when disturbance was aggregated in time, the negative effect was stronger relative to both F or I .