



University of the  
West of England

Wang, Y., Wen, S., Ellwood, M. D. F., Miller, A. and Chu, C. (2018)  
Temporal effects of disturbance on community composition in simu-  
lated stage-structured plant communities. *Ecology and Evolution*, 8  
(1). pp. 120-127. ISSN 2045-7758 Available from: <http://eprints.uwe.ac.uk/33745>

We recommend you cite the published version.

The publisher's URL is:

<http://dx.doi.org/10.1002/ece3.3660>

Refereed: Yes

(no note)

Disclaimer

UWE has obtained warranties from all depositors as to their title in the material deposited and as to their right to deposit such material.

UWE makes no representation or warranties of commercial utility, title, or fitness for a particular purpose or any other warranty, express or implied in respect of any material deposited.

UWE makes no representation that the use of the materials will not infringe any patent, copyright, trademark or other property or proprietary rights.

UWE accepts no liability for any infringement of intellectual property rights in any material deposited but will remove such material from public view pending investigation in the event of an allegation of any such infringement.

PLEASE SCROLL DOWN FOR TEXT.

1 **ORIGINAL RESEARCH**

2 **Temporal effects of disturbance on community composition in simulated**  
3 **stage-structured plant communities**

4 Youshi Wang<sup>1,#</sup>, Shujun Wen<sup>2,#</sup>, M. D. Farnon Ellwood<sup>3</sup>, Adam D. Miller<sup>4,5</sup>, and Chengjin Chu<sup>1,\*</sup>

5 <sup>1</sup> SYSU-Alberta Joint Lab for Biodiversity Conservation, Department of Ecology, State Key  
6 Laboratory of Biocontrol and School of Life Sciences, Sun Yat-sen University, Guangzhou  
7 510275, China

8 <sup>2</sup> Guangxi Key Laboratory of Plant Conservation and Restoration Ecology in Karst Terrain,  
9 Guangxi Institute of Botany, Guangxi Zhuang Autonomous Region and Chinese Academy of  
10 Sciences, Guilin 541006, China

11 <sup>3</sup> Centre for Research in Biosciences, University of the West of England, Coldharbour Lane,  
12 Bristol, BS16 1QY, UK

13 <sup>4</sup> Conservation Ecology Center; Smithsonian Conservation Biology Institute; National Zoological  
14 Park, Front Royal, VA, USA

15 <sup>5</sup> Institute for Sustainability, Energy, and Environment, University of Illinois, at  
16 Urbana-Champaign, Urbana, IL, USA

17

18 **Running title:** Disturbance and temporal compositional change

19 \*Corresponding author. Email: [chuchjin@mail.sysu.edu.cn](mailto:chuchjin@mail.sysu.edu.cn)

20 <sup>#</sup> Equal contribution to the work

## 21 **Abstract**

22 In an era of global environmental change, understanding how disturbance affects the dynamics of  
23 ecological communities is crucial. However, few studies have theoretically explored the potential  
24 influence of disturbance including both intensity and frequency on compositional change over  
25 time in communities with stage structure. A spatially explicit, individual-based model was  
26 constructed incorporating the various demographic responses to disturbance of plants at two  
27 different growth stages: seedlings and adults. In the model, we assumed that individuals within  
28 each stage were demographically equivalent (neutral) but differed between stages. We simulated  
29 a common phenomenon that seedlings suffered more from disturbance such as grazing and fire  
30 than adults. We showed how stage-structured communities of seedlings and adults responded to  
31 disturbance with various levels of disturbance frequency and intensity. In ‘undisturbed’  
32 simulations, the relationship between average species abundance (defined here as the total  
33 number of individuals divided by species richness) and community composition turnover  
34 (measured by the Bray-Curtis similarity index) was asymptotic. However, in strongly ‘disturbed’  
35 simulations with the between-disturbance intervals greater than one, this relationship became  
36 unimodal. Stage-dependent response to disturbance underlay the above discrepancy between  
37 undisturbed and disturbed communities.

38

39 **KEYWORDS:** compositional change, individual-based model, grid-based model, neutral model,  
40 stage structure

## 41 1 | INTRODUCTION

42 Understanding the increasingly severe impacts of natural and anthropogenic disturbance on the  
43 structure of communities is critical to conserve and manage what is left of the earth's natural  
44 biodiversity (Magurran 2007; Dornelas 2010). The precise mechanisms governing the  
45 relationship between disturbance and species richness, i.e. the intermediate hypothesis remain  
46 controversial (Fox 2013; Sheil and Burslem 2013), meanwhile the undeniable impacts of high  
47 levels of disturbance on species richness are becoming increasingly well documented (Connell  
48 1978; Bazzaz 1996; Kadmon and Benjamini 2006; Hughes *et al.* 2007; Bunn *et al.* 2010; Zhang  
49 *et al.* 2014).

50 The word *disturbance* is associated with ecological succession and often used generally,  
51 relating to any one of a range of specific phenomena such as the effects of fire, storms, or animal  
52 grazing on plants. From a theoretical perspective, all these sources can be unified under the  
53 concept of disturbance, because they eventually lead to modification of the fundamental  
54 demographic processes of individuals such as birth, death and immigration (Kadmon and  
55 Benjamini 2006; Dornelas 2010). These fundamental processes do more than govern the **number**  
56 of individuals per species (population growth); local extinctions and immigration govern the  
57 **number** of species per community (species richness), and the proportional abundance of each of  
58 those species. Besides species richness, we believe that evaluating temporal variations of  
59 community composition is fundamental to **understand** the essential biological mechanisms  
60 underlying population and community dynamics, which is another crucial dimension of

61 biodiversity (Pickett *et al.* 1987; Debussche *et al.* 1996).

62         In undisturbed plant communities decreasing average species abundance, defined as the  
63 total number of individuals divided by species richness, increases the average risk of local  
64 extinction through demographic stochasticity (Srivastava and Lawton 1998; Kadmon and  
65 Benjamini 2006; McGlynn *et al.* 2010). When average species abundance is small, communities  
66 experience a rapid turnover of species whether the community is saturated by individuals or not.  
67 It follows that when average species abundance is large, compositional turnover will **slow down**  
68 as communities reach saturation in terms of individuals. In this case, immigration from the  
69 regional species pool would contribute little to the composition of communities. **For instance, our**  
70 **previous work revealed an asymptotic relationship between average species abundance and the**  
71 **rate of compositional turnover (Wang *et al.* 2013). This implies that average species abundance**  
72 **could serve as a tractable and effective way of quantifying temporal effects of disturbance on**  
73 **community composition. Identifying a simple, robust parameter that can quantify the**  
74 **compositional turnover of communities will inform protocols for the conservation of biodiversity**  
75 **and land management.**

76         In disturbed plant communities, increased mortality caused by disturbance reduces the  
77 total individuals of communities (Sousa 1984; Dornelas 2010). Under these conditions  
78 demographic stochasticity leads to increased species turnover through time. It therefore makes  
79 intuitive sense that strongly disturbed communities should experience faster rates of species  
80 turnover than less disturbed ones. But disturbance also prevents communities from reaching

81 saturation in terms of individuals, releasing available resources to locally produced offspring and  
82 immigrants from the regional species pool, which will slow temporal turnover of communities  
83 (Kadmon and Benjamini 2006; Dornelas 2010). So far, how these two opposite processes jointly  
84 determine the community temporal turnover, and whether average species abundance could  
85 indicate temporal turnover remain unclear in disturbed communities.

86 To theoretically explore how disturbance influences community temporal dynamics, we  
87 constructed a stage-structured, spatially explicit individual-based model (IBM), in which every  
88 individual was labeled and the fundamental demographic processes determined the behavior of  
89 the communities. We modelled disturbance via manipulation of the mortality rates of seedlings  
90 rather than adults, thus incorporating the responses of different growth stages into the model  
91 (Suresh *et al.* 2010; Decocq *et al.* 2014). In the model, individuals within each stage were  
92 demographically equivalent (neutral) but differed between stages. We focused on how  
93 communities responded to a single disturbance event, as other studies did (Dornelas 2010). We  
94 used simulation experiments to answer the following two critical questions: 1) How disturbance  
95 intensity and frequency jointly influence community compositional change over time, and 2)  
96 Whether average species abundance could reflect the temporal turnover of composition in  
97 disturbed communities. Unless stated otherwise, we limited the application of average species  
98 abundance to indicate compositional change for communities with shared regional species pool.

99

## 100 2 | MATERIALS AND METHODS

101 The model description follows the ODD (Overview, Design concepts, Details) protocol for  
102 describing individual-based models (Grimm *et al.* 2006, 2010). Simulation experiments were  
103 implemented using NetLogo software (v5.0.4) (Wilensky 1999).

## 104 **2.1 | Purpose**

105 A stage-structured, spatially explicit individual-based model (IBM) was developed to explore the  
106 effect of disturbance (frequency and intensity) on the compositional change in stage-structured  
107 communities.

## 108 **2.2 | Entities, state variables and scales**

### 109 **2.2.1 | Individuals**

110 An individual in the model is characterized by the following state variables: species identity,  
111 spatial coordinates, birth rate ( $b$ ), death rate ( $m$ ), and age. Whether an individual gave rise to  
112 offspring depends on its age comparing to the threshold of maturity. For the sake of computation  
113 time here we set reproductive maturity to three years (The time of reproductive maturity did not  
114 qualitatively influence the simulation behavior).

### 115 **2.2.2 | Temporal resolution**

116 One time step in simulation experiments represents one year, with the one-year increase of age  
117 for survived individuals.

## 118 **2.3 | Process overview and scheduling**

119 Our model explicitly incorporates fundamental demographic processes, executed in order of  
120 ***Birth and Dispersal*** of offspring, ***Immigration*** (IM) from regional species pool ( $S$ ), and ***Death***.

121 These processes were described in detail in the section 2.7 for sub-models.

## 122 **2.4 | Design concepts**

### 123 **2.4.1 | Basic principles**

124 Neutral models of biodiversity have been extensively used in previous studies to investigate local  
125 community dynamics (Bell 2001; Hubbell 2001) and the effect of disturbance on species richness  
126 (Kadmon and Benjamini 2006). The model developed here is an extension of these models by  
127 incorporating stage-dependent demographic responses to disturbance.

### 128 **2.4.2 | Interaction**

129 Indirect competition for empty space exists among individuals, i.e. offspring and immigrants  
130 could only occupy the empty cells.

### 131 **2.4.3 | Stochasticity**

132 There are two stochastic components in the model: 1) The random spatial distribution of the  
133 individuals at model initialization, and 2) The random spatial location of empty cells recruited by  
134 the immigrants from regional species pool.

### 135 **2.4.4 | Observation**

136 The species composition of communities after a single disturbance event until the next  
137 disturbance was recorded.

## 138 **2.5 | Initialization**

139 We set up a landscape where the local community consists of  $A$  cells. The initial landscape was  
140 saturated, being occupied by all species present in the regional species pool, and with the number



141 of individuals for each species following a log-series distribution (Keddy 2005; Wang *et al.*  
142 2013). To avoid edge effects, a 'wraparound' approach (i.e. periodic or toroidal boundary  
143 conditions) was used (Chave *et al.* 2002).

## 144 **2.6 | Input data**

145 The model does not use input data to represent time-varying processes.

## 146 **2.7 | Sub-models**

### 147 **2.7.1 | Birth and Dispersal**

148 Every adult produces propagules at the rate  $b$ , which are classified as seedlings. Seedlings cannot  
149 produce offspring. We incorporated an intermediate type of dispersal of offspring into the  
150 simulations, this being a compromise between the extreme dispersal modes of local and global  
151 dispersal. Under this scenario, we assume that newborn offspring disperse according to a  
152 dispersal kernel taking the following form (Clark *et al.* 1999):

$$153 \quad K_{2Dt}(r) = \frac{2pr}{u[1+(r^2/u)]^{p+1}}, \quad p > 0$$

154 where  $u$  and  $p$  are parameters determining the shape of the function. This kernel combines  
155 Gaussian dispersal at short distances with a power-law tail of long-distance dispersal (Clark *et al.*  
156 1999; Chave *et al.* 2002).

### 157 **2.7.2 | Immigration**

158 To ensure that our model was biologically realistic, we accounted for the immigration of species  
159 from a regional species pool. The species abundance distribution (SAD) for species pool was set

160 to follow a log-series distribution (Gravel *et al.* 2006). At each time step, a fixed number  $IM$   
161 (immigration rate) of seedlings (equal to or less than  $IM$  species) were randomly drawn with  
162 replacement from the species pool, and globally dispersed at random into the local community.  
163 Both dispersing offspring and immigrants could only colonize vacant sites.

### 164 **2.7.3 | Death**

165 Having set  $m_{young}$  and  $m_{old}$  as the intrinsic mortality rates for seedlings and adults, we set  $m_{young}$  at  
166 a higher level than  $m_{old}$ , to account for the fact that seedling mortality usually exceeds that of  
167 adults (Suresh *et al.* 2010). In our simulations, we set  $m_{young}$  at 1.2 times greater than  $m_{old}$ .

168         Though different definitions of disturbance have been proposed, one fundamental  
169 outcome of disturbance is the increased mortality of individuals (Sousa 1984; Dornelas 2010).  
170 For instance, some empirical studies have demonstrated that seedlings are more sensitive to  
171 environmental change/disturbance than adults (Sukumar *et al.* 2005; Suresh *et al.* 2010; Decocq  
172 *et al.* 2014). Such differential responses of different demographic stages to disturbance are  
173 ubiquitous in nature (Suresh *et al.* 2010; Decocq *et al.* 2014; Green *et al.* 2014). To incorporate  
174 this feature into the model, we assume that disturbance increases the mortality rate of seedlings  
175 but has ignorable effect on adults. This assumption mimics well various types of disturbance  
176 events in natural communities, including the grazing and fire in forests (Sukumar *et al.* 2005;  
177 Edwards and Krochenberger 2006). Thus, the seedling mortality rate under disturbance is  
178  $D \times m_{young}$ , where  $D$  represents disturbance intensity.  $D = 1$  means that no disturbance occurs.  
179 Seedlings in the simulated community have identical mortality rates ( $D \times m_{young}$ ), and adults have

180 identical birth rates ( $b$ ) and mortality rates ( $m_{old}$ ).

181         Each individual experienced a corresponding risk of mortality, depending on the stage the  
182 individual belongs to. By comparing the realized mortality rate of seedlings ( $D \times m_{young}$ ) or  $m_{old}$  to  
183 a random number from a  $[0, 1]$  uniform distribution, we determined the fate of the focal  
184 individual in terms of its survival; when effective mortality is greater than the random sample,  
185 then the individual is killed.

## 186 **2.8 | Simulation experiments and data analysis**

187 We conducted a set of factorial simulations within the following parameter space: birth rate  $b$  for  
188 all species ranges from 0.1 to 2.7 with the interval 0.2; death rate of adults  $m_{old} = 0.05, 0.1,$  and  
189 0.15; immigration rate  $IM = 20$  and 60. We simulated three levels of disturbance intensity for  
190 each parameter setting:  $D = 1.0, 3.0,$  and 5.0. Model parameters, their meanings and values taken  
191 were summarized in Table 1. All simulations for undisturbed communities were run for 10 000  
192 time steps in order to allow communities to reach a dynamical equilibrium state in terms of  
193 species richness. We set identical simulation time for communities suffering from disturbance.

194         To explore the responses of communities to disturbance, we recorded the species  
195 composition of communities after a single disturbance event until the next disturbance. In  
196 addition, previous studies have demonstrated that disturbance frequency and intensity might  
197 interact to influence community structure (Miller *et al.* 2011; Hall *et al.* 2012). To this end, we  
198 conducted additional simulations with different frequencies of disturbance. In addition, due to the  
199 potential interactions between disturbance frequencies and reproductive maturity of seedlings

200 (three years), we set up three scenarios with the disturbance frequencies ( $F$ ) smaller (one year)  
201 and larger than (five years), and equal to (three years) the maturity, respectively. We used the  
202 Bray-Curtis similarity index (Bray and Curtis 1957) calculated in the package *fossil* (Vavrek 2011)  
203 on the R platform (R Development Core Team 2014) to quantify compositional changes of  
204 communities across time, as this index accounts for both the incidence and the abundance of each  
205 species. The larger the Bray-Curtis similarity value, the more similar the community composition.  
206 We used the average species abundance (ASA), i.e. the total number of individuals divided by  
207 species richness, and coefficients of variation (CV) of species abundance for the disturbed  
208 community to indicate the compositional change of this community across time until the next  
209 disturbance event. Take the scenario with the frequency with three years as an example. After 10  
210 000 startup steps, we compared the compositional change between the disturbed community at  
211 the step of 10 002 ( $t_0$ ) and the communities followed without disturbance at the steps of 10 003  
212 ( $t_1$ ) and 10 004 ( $t_2$ ), respectively. This is for one disturbance event. Similarly, we compared the  
213 compositional change between the disturbed community at the step of 10 005 ( $t_0$ ) and the  
214 communities followed without disturbance at the steps of 10 006 ( $t_1$ ) and 10 007 ( $t_2$ ). We repeated  
215 this processes until 50 disturbance events recorded, and Bray-Curtis similarity values, average  
216 species abundance and CVs of species abundance were obtained by averaging individual values  
217 across 50 disturbance events and across ten replicates.

218

219 **3 | RESULTS**

220 Simulations of undisturbed communities (the disturbance intensity  $D = 1.0$ ) show that increasing  
221 birth rates increase the number of individuals in the community (Fig. 1A). Species richness  
222 increased slightly and then decreased sharply (Fig. 1B), resulting in a hump-shaped curve between  
223 community size (total number of individuals) and species richness (Fig. 1C). Simulations of  
224 disturbed communities generated similar unimodal patterns.

225         The compositional change over time was presented in Fig. 2 for the scenario with the  
226 disturbance frequency ( $F$ ) equal to five years and the disturbance intensity ( $D$ ) equal to three.  
227 Bray-Curtis similarity values increased with the time after disturbance, especially when average  
228 species abundance was low. Under no disturbance ( $D = 1.0$ ), asymptotic curves emerged between  
229 average species abundance and Bray-Curtis similarity in all three scenarios of disturbance  
230 frequency (Fig. 3). When the disturbance occurred every year, the relationships between average  
231 species abundance and similarity displayed asymptotic patterns as well but with faster  
232 compositional change (Fig. 3A). However, when the disturbance frequencies were larger than **one**  
233 (three and five years), especially for communities suffering from strong disturbance ( $D = 5.0$ ), the  
234 Bray-Curtis similarity values firstly increased then decreased (Fig. 3B, Fig. 3D). Such unimodal  
235 patterns gradually disappeared over time until the next disturbance event (Figs. 3B-3C for the  
236 disturbance frequency of three years, and Figs. 3D-3G for the disturbance frequency of five years).  
237 Relationships between CV of species abundance and Bray-Curtis similarity displayed similar  
238 patterns described above (See Fig. S1 in the Supporting Information).

## 239 **4 | DISCUSSIONS**

240 As we expected, the simulated relationship between average species abundance and species  
241 turnover was asymptotic for undisturbed communities (Fig. 3). In unsaturated communities, in line  
242 with the more individuals hypothesis, larger average species abundance on average reduced the  
243 likelihood of stochastic extinctions (Srivastava and Lawton 1998; Kadmon and Benjamini 2006;  
244 McGlynn *et al.* 2010). Under these conditions the temporal turnover of species **slowed down**, and  
245 communities became more similar through time. However, in saturated communities, increasing  
246 birth rates expanded average species abundance that then had little effect on species composition  
247 as the communities grew asymptotically towards saturation in terms of individuals (Fig. 3). In this  
248 case, community composition was mainly dominated by locally produced offspring. Since the  
249 immigration rates were fixed, immigrants from the regional species pool contributed little to  
250 compositional change. This pattern is linked to the dilution effect (Kadmon and Benjamini 2006),  
251 where the ratio between locally produced individuals and immigrants influence the number of  
252 species that coexist in a given community.

253         What effect does disturbance have on the relationship between species turnover and  
254 average species abundance? The results showed that disturbed communities experienced faster  
255 species turnover than undisturbed communities (Fig. 3). Disturbance caused increased mortality  
256 among seedlings, reduced average species abundance, reduced total number of individuals, and  
257 prevented communities reaching saturation in terms of individuals (Fig. 1A). This finding is  
258 consistent with a previous study showing that disturbed forests experienced a greater turnover of  
259 functional traits than expected (Swenson *et al.* 2012). When the between-disturbance intervals

260 were larger than one, for comparisons between disturbed communities and ones closely followed  
261 ( $t_0-t_1$  for the case of disturbance frequency equal to three years, and  $t_0-t_1$  and  $t_0-t_2$  for the case of  
262 disturbance frequency equal to five years), disturbance also caused the asymptotic relationship  
263 between community similarity and average species abundance to become unimodal (Figs. 3B, 3D  
264 and 3E); this unimodal curve showed community similarity decreasing as average species  
265 abundance increased. In disturbed communities, as in undisturbed communities, there existed an  
266 initial positive phase between average species abundance and community similarity (Fig. 3). This  
267 initial phase suggests that stochastic extinctions were becoming less likely as average species  
268 abundance increased (Srivastava and Lawton 1998; McGlynn *et al.* 2010). From this we can  
269 conclude that, regardless of disturbance, demographic stochasticity is the main driver of species  
270 turnover at low average species abundance. But it was the emergence of the negative, decreasing  
271 phase in strongly disturbed communities that we found most interesting, attributing this to the  
272 influence of disturbance on seedling mortality. While increasing the birth rates of adults led to an  
273 increased number of seedlings and larger communities, disturbance had relatively minor influence  
274 on species richness (Fig. 1B). In our simulations, we assumed that disturbance only increased the  
275 mortality rate of seedlings. This implied that for a given species even if all seedlings were killed  
276 by disturbance, the survival of its adults maintain species' persistence in communities, which  
277 explained the minor change of disturbance on species richness. Thus, we could speculate that  
278 similarity indices only considering presence-absence information would have a lower probability  
279 to detect the decreasing trend between average species abundance and compositional change.

280 Simulated communities with larger average species abundance had more seedlings than ones with  
281 smaller average species abundance. When disturbance occurred, more seedlings in disturbed  
282 communities with larger average species abundance were killed and left more vacant space for  
283 new seedlings (offspring of local adults and immigrants from regional pool), which led to faster  
284 turnover measured by the Bray-Curtis similarity index taking account of species abundance (Figs.  
285 3B, 3D and 3E). This legacy effect of disturbance gradually waned over time away disturbance  
286 events (Figs. 3C, 3F, and 3G).

287 Many empirical studies of heavily disturbed plant communities have attempted to explore  
288 the causes and consequences of disturbance on population dynamics and community structure  
289 (Sukumar *et al.* 2005; Suresh *et al.* 2010). For instance, in the Mudumalai permanent forest  
290 dynamics plot, the causes of disturbance in this region were categorized into three groups: Death  
291 of the aboveground stems caused by fire, herbivory by elephants, and other natural causes  
292 including the effects of drought, windfall, and disease (Suresh *et al.* 2010). It has been  
293 demonstrated that the effects of these types of disturbance on demographic rates are strongly  
294 stage-dependent (Suresh *et al.* 2010). In other words, smaller individuals suffer more than larger  
295 individuals, especially under elephant herbivory. Suresh *et al.* (2010) attributed the mortality of  
296 small to medium woody stems in this forest plot mostly to these factors. In line with our  
297 simulations of strongly disturbed communities, empirical evidence from the Mudumalai plot  
298 confirms that increasing average species abundance increases rather than decreases species  
299 turnover and compositional similarity. These results contrast with the undisturbed simulations.



300           Though we accounted for just two stages (seedlings and adults) in the model, our  
301 stage-structured simulations captured the essential demographic effects of disturbance on  
302 individuals in many natural communities where seedlings suffer more from disturbance than  
303 adults. Potential refinements to our model would be to 1) Incorporate species-specific responses to  
304 disturbance through the variability of demographic rates between species, to release the  
305 assumption of neutrality of our model (Walker *et al.* 2003), 2) Explicitly simulate the growth of  
306 individuals resulting in continuous size distribution rather than two discrete stages in the present  
307 work, and 3) Explore the impact of different types of stage-dependent responses to disturbance,  
308 such as the scenario of adults suffering more than seedlings in terms of extreme drought (Bennett  
309 *et al.* 2015; Meakem *et al.* 2017).

310

## 311 **ACKNOWLEDGEMENTS**

312 This study was financially supported by the National Key R&D Program of China  
313 (2017YFC0506101) and the National Natural Science Foundation of China (31570426 and  
314 31622014) to CC. MDFE was supported by UWE Research Excellence Funding. ADM was  
315 supported by DOE grant #DE-SC0010039/ #DE-SC0008085.

316

## 317 **CONFLICT OF INTEREST**

318 None declared.

319

---

320 **AUTHOR CONTRIBUTIONS**

321 YW, SW, and CC conceived and designed the study, and wrote the manuscript with input from

322 MDFE and ADM contributed.

323 **REFERENCES**

- 324 **Bazzaz FA. 1996.** *Plants in Changing Environments: Linking Physiological, Population, and*  
325 *Community Ecology*. Cambridge University Press, Cambridge, U.K.
- 326 **Bell G. 2001.** Neutral macroecology. *Science* **293**: 2413–2418.
- 327 **Bennett AC, McDowell NG, Allen CD, Anderson-Teixeira KJ. 2015.** Larger trees suffer  
328 most during drought in forests worldwide. *nature Plants* **1**: 15139.
- 329 **Bunn WA, Jenkins MA, Brown CB, Sanders NJ. 2010.** Change within and among forest  
330 communities: the influence of historic disturbance, environmental gradients, and  
331 community attributes. *Ecography* **33**: 425–434.
- 332 **Chave J, Muller-Landau HC, Levin SA. 2002.** Comparing classical community models:  
333 Theoretical consequences for patterns of diversity. *American Naturalist* **159**: 1–23.
- 334 **Clark JS, Silman M, Kern R, Macklin E, HilleRisLambers J. 1999.** Seed dispersal near and  
335 far: patterns across temperate and tropical forests. *Ecology* **80**: 1475–1494.
- 336 **Connell J. 1978.** Diversity in tropical rain forests and coral reefs. *Science* **199**: 1302–1310.
- 337 **Debussche M, Escarré J, Lepart J, Houssard C, Lavorel S. 1996.** Changes in  
338 Mediterranean plant succession: old-fields revisited. *Journal of Vegetation Science* **7**:  
339 519–526.
- 340 **Decocq G, Beina D, Jamoneau A, Gourlet-Fleury S, Closset-Kopp D. 2014.** Don't miss the  
341 forest for the trees! Evidence for vertical differences in the response of plant diversity to  
342 disturbance in a tropical rain forest. *Perspectives in Plant Ecology, Evolution and Systematics*  
343 **16**: 279–287.
- 344 **Dornelas M. 2010.** Disturbance and change in biodiversity. *Philosophical Transactions of*  
345 *the Royal Society B: Biological Sciences* **365**: 3719–3727.
- 346 **Edwards W, Krochenberger A. 2006.** Seedling mortality due to drought and fire  
347 associated with the 2002 El Niño event in a tropical rain forest in North-East Queensland,  
348 Austria. *Biotropica* **38**: 16–26.
- 349 **Fox J. 2013.** The intermediate disturbance hypothesis should be abandoned. *Trends in*  
350 *Ecology & Evolution* **28**: 86–92.
- 351 **Gravel D, Canham CD, Beaudet M, Messier C. 2006.** Reconciling niche and neutrality: The

- 352 continuum hypothesis. *Ecology Letters* **9**: 399–409.
- 353 **Green PT, Harms KE, Connell JH. 2014.** Nonrandom, diversifying processes are  
354 disproportionately strong in the smallest size classes of a tropical forest. *Proceedings of the*  
355 *National Academy of Sciences* **111**: 18649–18654.
- 356 **Grimm V, Berger U, Bastiansen F, et al. 2006.** A standard protocol for describing  
357 individual-based and agent-based models. *Ecological Modelling* **198**: 115–126.
- 358 **Grimm V, Berger U, DeAngelis DL, Polhill JG, Giske J, Railsback SF. 2010.** The ODD  
359 protocol: A review and first update. *Ecological Modelling* **221**: 2760–2768.
- 360 **Hubbell SP. 2001.** *The unified neutral theory of biodiversity and biogeography*. Princeton  
361 University Press, Princeton, NJ.
- 362 **Hughes AR, Byrnes JE, Kimbro DL, Stachowicz JJ. 2007.** Reciprocal relationships and  
363 potential feedbacks between diversity and disturbance. *Ecology Letters* **10**: 849–864.
- 364 **Kadmon R, Benjamini Y. 2006.** Effects of productivity and disturbance on species richness:  
365 a neutral model. *American Naturalist* **167**: 939–946.
- 366 **Keddy P. 2005.** Putting the plants back into plant ecology: six pragmatic models for  
367 understanding and conserving plant diversity. *Annals of Botany* **96**: 177–189.
- 368 **Magurran AE. 2007.** Species abundance distributions over time. *Ecology Letters* **10**:  
369 347–354.
- 370 **McGlynn TP, Weiser MD, Dunn RR. 2010.** More individuals but fewer species: testing the  
371 “more individuals hypothesis” in a diverse tropical fauna. *Biology Letters* **6**: 490–493.
- 372 **Meakem V, Tepley AJ, Gonzalez-Akre EB, et al. 2017.** Role of tree size in moist tropical  
373 forest carbon cycling and water deficit responses. *New Phytologist*: In press.
- 374 **Pickett STA, Collins SL, Armesto JJ. 1987.** Models, mechanisms and pathways of  
375 succession. *The Botanical Review* **53**: 335–371.
- 376 **R Development Core Team. 2014.** R: A Language and Environment for Statistical  
377 Computing. Vienna, Austria: R Foundation for Statistical Computing.
- 378 **Sheil D, Burslem DFRP. 2013.** Defining and defending Connell’s intermediate disturbance  
379 hypothesis: a response to Fox. *Trends in Ecology & Evolution* **28**: 571–572.
- 380 **Sousa WP. 1984.** The role of disturbance in natural communities. *Annual Review of Ecology*

- 381 *and Systematics* **15**: 353–391.
- 382 **Srivastava DS, Lawton JH. 1998.** Why more productive sites have more species: An  
383 experimental test of theory using tree-hole communities. *American Naturalist* **152**:  
384 510–529.
- 385 **Sukumar R, Suresh HS, Dattaraja HS, Srinidhi S, Nath C. 2005.** Dynamics of a tropical dry  
386 forest at Mudumalai (India): climate, fire, elephants and the evolution of life history  
387 strategies. In: *Biotic interactions in the tropics: Their role in the maintenance of species*  
388 *diversity* (Eds Burslem D., Pinard M., Hartley S.). Cambridge University Press, Cambridge, U.K.,  
389 510–529.
- 390 **Suresh HS, Dattaraja HS, Sukumar R. 2010.** Relationship between annual rainfall and tree  
391 mortality in a tropical dry forest: Results of a 19-year study at Mudumalai, southern India.  
392 *Forest Ecology and Management* **259**: 762–769.
- 393 **Swenson NG, Stegen JC, Davies SJ, et al. 2012.** Temporal turnover in the composition of  
394 tropical tree communities: functional determinism and phylogenetic stochasticity. *Ecology*  
395 **93**: 490–499.
- 396 **Vavrek M. 2011.** fossil: Palaeoecological and palaeogeographical analysis tools.  
397 *Palaeontologia Electronica* **14**: 1T:16p.
- 398 **Walker LR, Lodge DJ, Guzmín-Grajales SM, Fetcher N. 2003.** Species-specific seedling  
399 responses to hurricane disturbance in a Puerto Rican rain forest. *Biotropica* **35**: 472–485.
- 400 **Wang YS, Yang ZY, Zhou SR, et al. 2013.** The effects of positive interactions on temporal  
401 turnover of community composition along an environmental gradient. *PLoS ONE* **8**: e78698.  
402 doi:10.1371/journal.pone.0078698.
- 403 **Wilensky U. 1999.** NetLogo. <http://ccl.northwestern.edu/netlogo/>. Center for connected  
404 learning and computer-based modeling. *Northwestern University*.
- 405 **Zhang J, Mayor SJ, He FL. 2014.** Does disturbance regime change community assembly of  
406 angiosperm plant communities in the boreal forest? *Journal of Plant Ecology* **7**: 188–201.
- 407
- 408

---

409 **SUPPORTING INFORMATION**

410 Supplementary data consist of four figures:

411 **Figure S1.** Relationships between CV of species abundance and Bray-Curtis similarity values  
412 from simulations with the immigration rate equal to 60.

413 **Figure S2.** Influence of birth rate on community metrics for the scenario with the immigration  
414 rate equal to 20.

415 **Figure S3.** Compositional change of simulated communities over time for the scenario with the  
416 immigration rate equal to 20.

417 **Figure S4.** Simulated patterns between average species richness and temporal compositional  
418 change for the scenario with the immigration rate equal to 20.

419

420 **Table 1.** Model parameters, their meanings and values taken.

Parameter	Meaning	Values
$A$	Landscape size	$100 \times 100$ cells
$S$	Regional species pool	200 species
$IM$	Immigration rate	20 and 60 individuals
$b$	Birth rate	0.1~ 2.7, with the interval of 0.2
$m_{old}$	Intrinsic death rate for adults	0.05, 0.1, and 0.15
$m_{young}$	Intrinsic death rate for seedlings	$1.2 \times m_{old}$
$D$	Disturbance intensity	1.0, 3.0, and 5.0
$F$	Disturbance frequency	1.0, 3.0, and 5.0

421 **Note:** We conducted a total of 7 560 simulations: 10 replicates  $\times$  3 levels of disturbance  
422 frequency ( $F = 1.0, 3.0,$  and  $5.0$ )  $\times$  3 levels of disturbance intensity ( $D = 1.0, 3.0,$  and  $5.0$ )  $\times$  2  
423 levels of immigration ( $IM = 20$  and  $60$ )  $\times$  14 levels of birth rate ( $b$  is from 0.1 to 2.7 with the  
424 interval of 0.2)  $\times$  3 levels of death rate ( $m_{old} = 0.05, 0.1,$  and  $0.15$ ). The results presented (Figures  
425 1 to 3) are based on the setting with mortality rate 0.1, regional species pool 200, and  
426 immigration rate 60 (See Figs. S2-S4 in the Supporting Information for results with the  
427 immigration rate equal to 20).

428

429

**Figure captions**

430

431

432

433

434

435

436

437

438

439

440

441

442

443

444

445

446

447

448

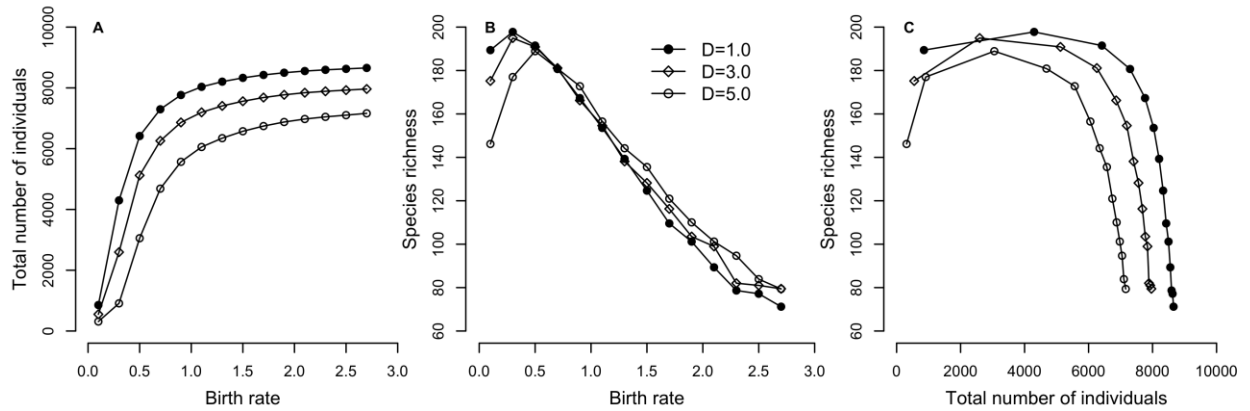
**Figure 1.** Influence of birth rate on community metrics. (A) Simulated relationships between birth rate and the total number of individuals, (B) Simulated relationships between birth rate and species richness, and (C) Simulated relationships between the total number of individuals and species richness. Three levels of disturbance intensity were explored:  $D = 1.0$ ,  $3.0$ , and  $5.0$ .  $D = 1.0$  means no disturbance. The case with the disturbance frequency equal to two years was presented as an example here. **Immigration rate is equal to 20.** Each data point represents the mean of ten replicates for each parameter combination.

**Figure 2.** Compositional change of simulated communities over time. The case with the disturbance frequency ( $F$ ) equal to five years and disturbance intensity ( $D$ ) equal to three was presented as an example here. **ASA obtained at  $t_0$**  represents average species abundance determined by demographic processes as a result of disturbance. The labels of  $t_0-t_1$ ,  $t_0-t_2$ ,  $t_0-t_3$ , and  $t_0-t_4$  represent the comparisons between the disturbed community ( $t_0$ ) and the communities one, two, three and four years after a disturbance event. **Immigration rate is equal to 20.** Each data point represents the mean of ten replicates for each parameter combination.

**Figure 3.** Simulated patterns between average species abundance and temporal compositional change measured by Bray-Curtis similarity (A, the disturbance frequency equal to one year; B-C, the disturbance frequency equal to three years; D-G, the disturbance frequency equal to five



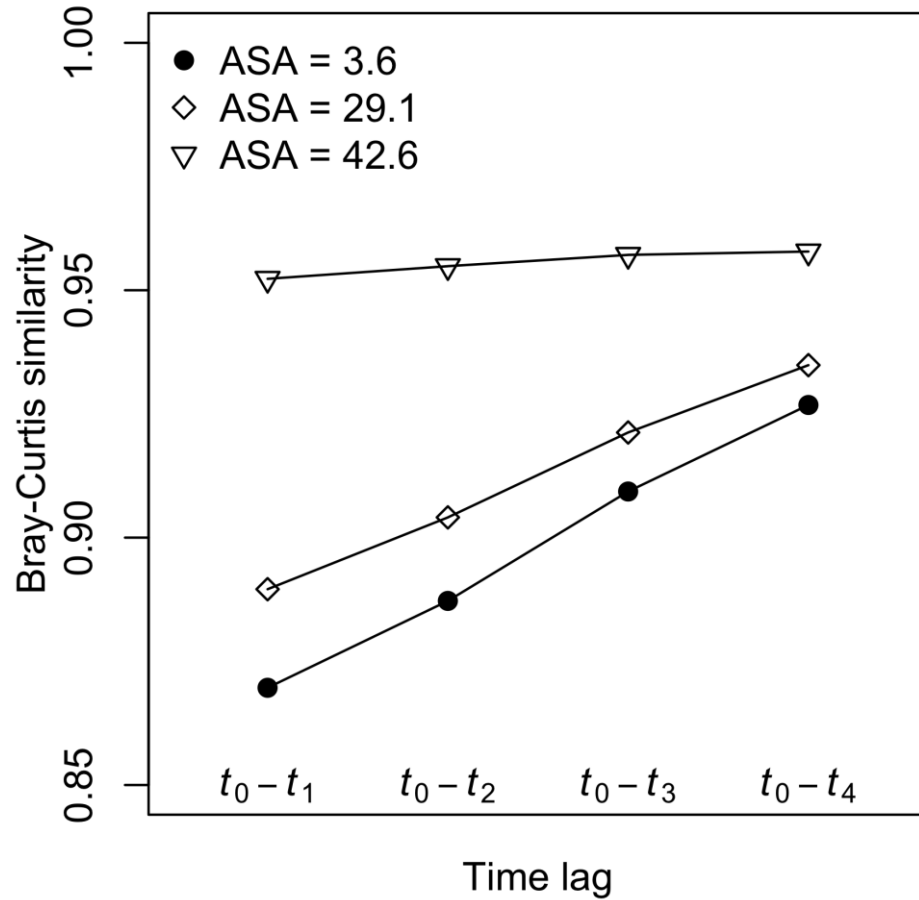
449 years). Three levels of disturbance intensity were explored:  $D = 1.0, 3.0,$  and  $5.0$ . The maturity  
450 time for seedlings was equal to three years. The labels of  $t_0-t_1, t_0-t_2, t_0-t_3,$  and  $t_0-t_4$  represent the  
451 comparisons between the disturbed community ( $t_0$ ) and the communities one, two, three and four  
452 years after a disturbance event. **Immigration rate is equal to 20.** Each data point represents the  
453 mean of ten replicates for each parameter combination.



454

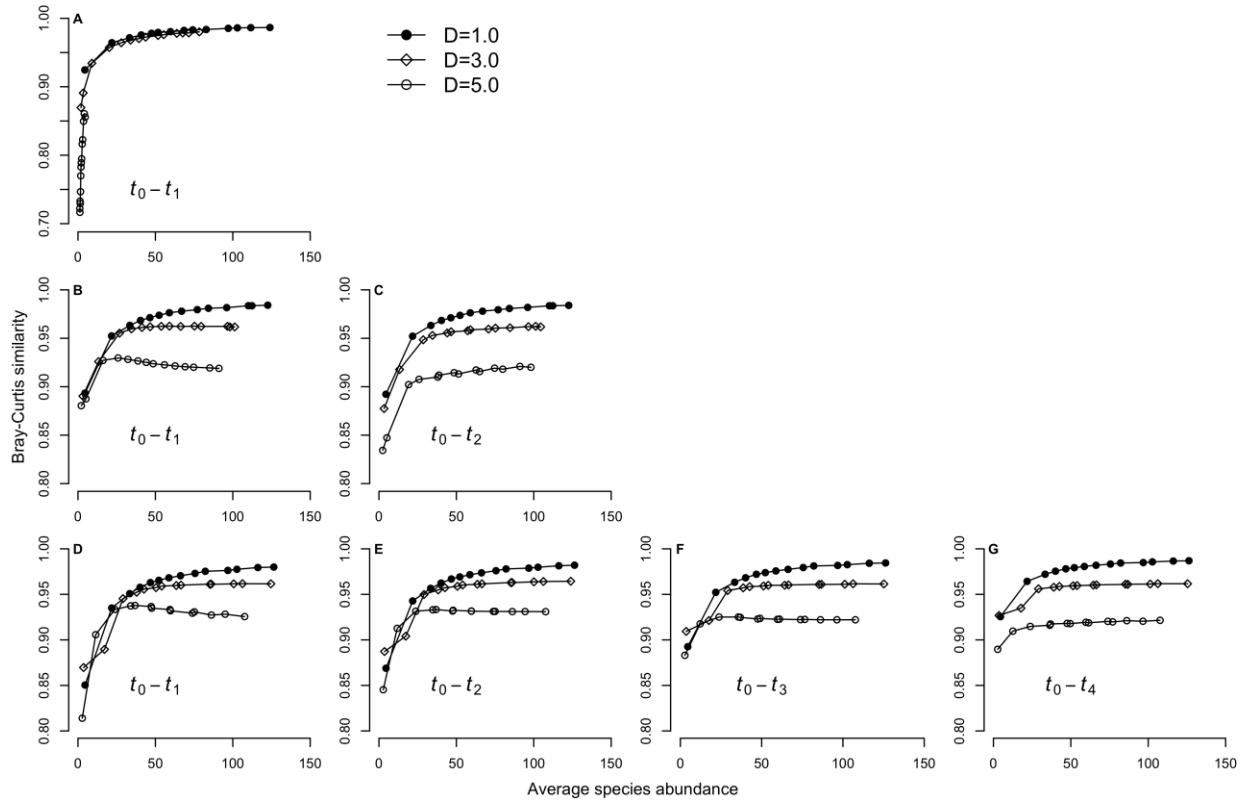
455 **Figure 1.** Influence of birth rate on community metrics. (A) Simulated relationships between  
 456 birth rate and the total number of individuals, (B) Simulated relationships between birth rate and  
 457 species richness, and (C) Simulated relationships between the total number of individuals and  
 458 species richness. Three levels of disturbance intensity were explored:  $D = 1.0$ , 3.0, and 5.0.  $D =$   
 459 1.0 means no disturbance. The case with the disturbance frequency equal to two years was  
 460 presented as an example here. **Immigration rate is equal to 20.** Each data point represents the  
 461 mean of ten replicates for each parameter combination.

462



463

464 **Figure 2.** Compositional change of simulated communities over time. The case with the  
 465 disturbance frequency ( $F$ ) equal to five years and disturbance intensity ( $D$ ) equal to three was  
 466 presented as an example here. ASA obtained at  $t_0$  represents average species abundance  
 467 determined by demographic processes as a result of disturbance. The labels of  $t_0-t_1$ ,  $t_0-t_2$ ,  $t_0-t_3$ , and  
 468  $t_0-t_4$  represent the comparisons between the disturbed community ( $t_0$ ) and the communities one,  
 469 two, three and four years after a disturbance event. Immigration rate is equal to 20. Each data  
 470 point represents the mean of ten replicates for each parameter combination.



471

472 **Figure 3.** Simulated patterns between average species abundance and temporal compositional  
 473 change measured by Bray-Curtis similarity (A, the disturbance frequency equal to one year; B-C,  
 474 the disturbance frequency equal to three years; D-G, the disturbance frequency equal to five  
 475 years). Three levels of disturbance intensity were explored:  $D = 1.0$ ,  $3.0$ , and  $5.0$ . The maturity  
 476 time for seedlings was equal to three years. The labels of  $t_0-t_1$ ,  $t_0-t_2$ ,  $t_0-t_3$ , and  $t_0-t_4$  represent the  
 477 comparisons between the disturbed community ( $t_0$ ) and the communities one, two, three and four  
 478 years after a disturbance event. **Immigration rate is equal to 20.** Each data point represents the  
 479 mean of ten replicates for each parameter combination.