1 **ORIGINAL RESEARCH**

2 **Temporal effects of disturbance on community composition in simulated**

3 **stage-structured plant communities**

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

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Abstract

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

1 | INTRODUCTION

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

The word *disturbance* is associated with ecological succession and often used generally, relating to any one of a range of specific phenomena such as the effects of fire, storms, or animal grazing on plants. From a theoretical perspective, all these sources can be unified under the concept of disturbance, because they eventually lead to modification of the fundamental demographic processes of individuals such as birth, death and immigration (Kadmon and Benjamini 2006; Dornelas 2010). These fundamental processes do more than govern the number of individuals per species (population growth); local extinctions and immigration govern the number of species per community (species richness), and the proportional abundance of each of those species. Besides species richness, we believe that evaluating temporal variations of community composition is fundamental to understand the essential biological mechanisms 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     $$K_{2Dt}(r) = \frac{2\,p\,r}{u\,[1+(r^2/u)]^{p+1}}, \quad p > 0$$

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).

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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.

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406   angiosperm plant communities in the boreal forest? *Journal of Plant Ecology* **7**: 188–201.

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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	100×100 cells
S	Regional species pool	200 species
IM	Immigration rate	20 and 60 individuals
b	Birth rate	$0.1 \sim 2.7$, 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 × 3 levels of disturbance

422   frequency ($F = 1.0, 3.0$, and 5.0) × 3 levels of disturbance intensity ($D = 1.0, 3.0$, and 5.0) × 2

423   levels of immigration ($IM = 20$ and 60) × 14 levels of birth rate (b is from 0.1 to 2.7 with the

424   interval of 0.2) × 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).

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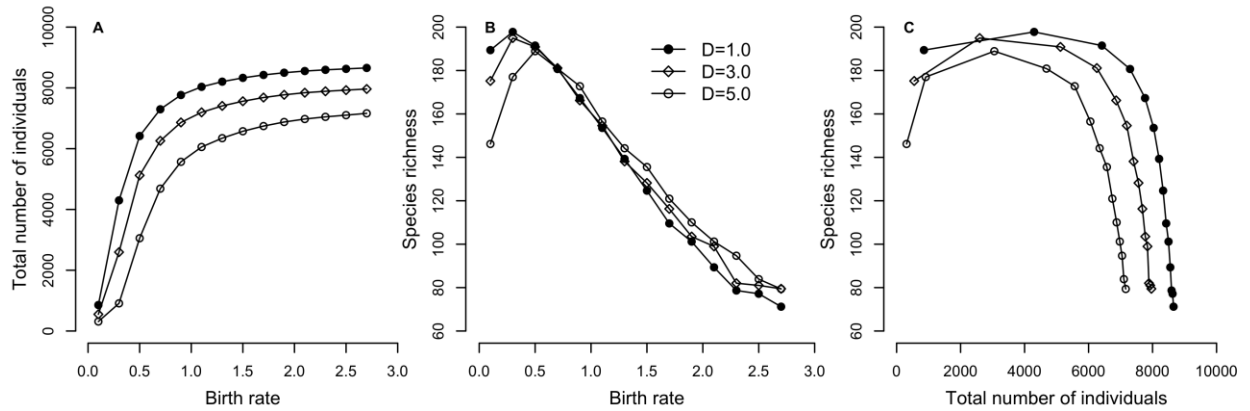
429 **Figure captions**

430 **Figure 1.** Influence of birth rate on community metrics. (A) Simulated relationships between

431 birth rate and the total number of individuals, (B) Simulated relationships between birth rate and

432 species richness, and (C) Simulated relationships between the total number of individuals and

433 species richness. Three levels of disturbance intensity were explored: $D = 1.0$, 3.0, and 5.0. $D =$

434 1.0 means no disturbance. The case with the disturbance frequency equal to two years was

435 presented as an example here. Immigration rate is equal to 20. Each data point represents the

436 mean of ten replicates for each parameter combination.

437

438 **Figure 2.** Compositional change of simulated communities over time. The case with the

439 disturbance frequency (F) equal to five years and disturbance intensity (D) equal to three was

440 presented as an example here. ASA obtained at t_0 represents average species abundance

441 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

442 t_0-t_4 represent the comparisons between the disturbed community (t_0) and the communities one,

443 two, three and four years after a disturbance event. Immigration rate is equal to 20. Each data

444 point represents the mean of ten replicates for each parameter combination.

445

446 **Figure 3.** Simulated patterns between average species abundance and temporal compositional

447 change measured by Bray-Curtis similarity (A, the disturbance frequency equal to one year; B-C,

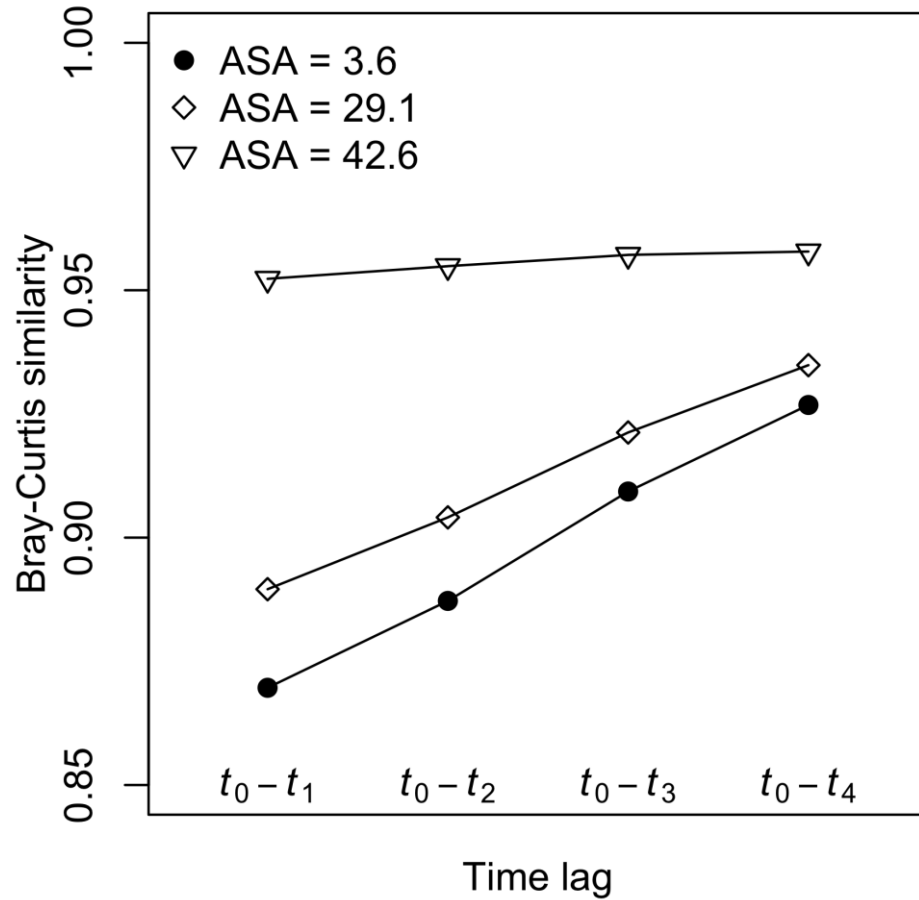448 the disturbance frequency equal to three years; D-G, the disturbance frequency equal to five

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
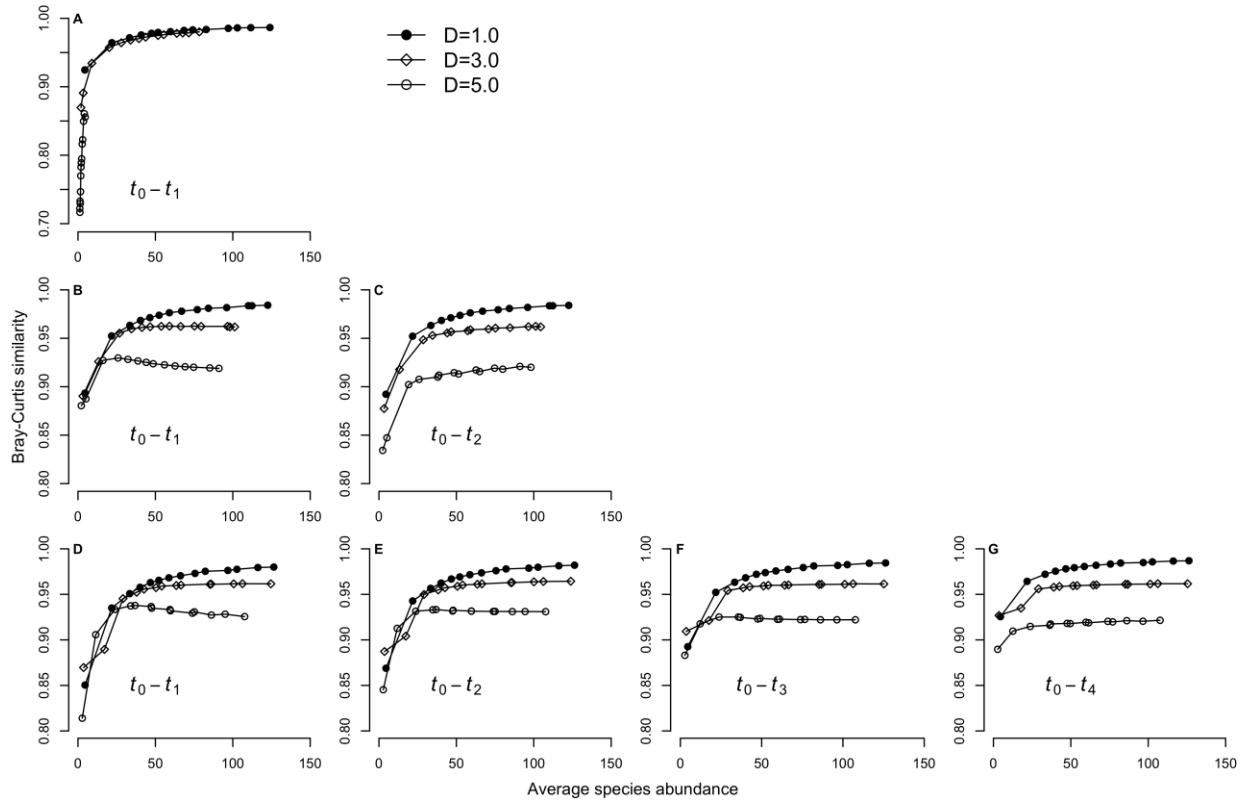
453   mean of ten replicates for each parameter combination.

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.

471

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

years). Three levels of disturbance intensity were explored: $D = 1.0$, 3.0, and 5.0. The maturity

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

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.